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AN ANALYSIS OF CARRYING BEHAVIOUR IN THE
COMMON MARMOSET (*Callithrix jacchus*).

A thesis submitted for the degree of
Master of Philosophy

from

The Open University

January 1991

by

Fiona M Clarke BSc. (Hons.)
University of Sussex

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This thesis is dedicated to the memory of Paul Ivor Clarke.

6-4-1931 to 9-12-1977



This thesis is dedicated to the memory of Paul Ivor Clarke.

6-4-1931 to 9-12-1977

A B S T R A C T

Marmosets (*Callithrix jacchus*) give birth to infants, usually twins, and the mother can become pregnant again almost immediately, so the female is lactating, to feed the newly born infants, while pregnant. These conditions impose extreme physiological demands upon the mother; all the adult and subadult members of the family help to care for the infants, in many instances, from the day of birth. The adult males and adolescents play a very important role in the care of the infants and in their socialisation.

The effects of carrying infants on the behaviour of the mother and the other caregivers were investigated. Identified members of families of marmosets were observed in the first two weeks after the infant's birth, and again in the fifth to sixth weeks of their life. The movements of the caregivers were quantified, as were the duration of the carrying bouts. Carrying one infant and carrying as a pair were scored individually. Carrying infants was found to have a profound effect upon their mobility and activity levels. The adults, and subadult siblings, tended to carry the infants as a pair rather than consecutively. In this way the caregivers, although burdened by the infants, may be maximising the time spent in enforced inactivity by carrying the infants together.

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A B S T R A C T

Marmosets (*Callithrix jacchus*) give birth to infants, usually twins, and the mother can become pregnant again almost immediately, so the female is lactating, to feed the newly born infants, while pregnant. These conditions impose extreme physiological demands upon the mother; all the adult and subadult members of the family help to care for the infants, in many instances, from the day of birth. The adult males and adolescents play a very important role in the care of the infants and in their socialisation.

The effects of carrying infants on the behaviour of the mother and the other caregivers were investigated. Identified members of families of marmosets were observed in the first two weeks after the infant's birth, and again in the fifth to sixth weeks of their life. The movements of the caregivers were quantified, as were the duration of the carrying bouts. Carrying one infant and carrying as a pair were scored individually. Carrying infants was found to have a profound effect upon their mobility and activity levels. The adults, and subadult siblings, tended to carry the infants as a pair rather than consecutively. In this way the caregivers, although burdened by the infants, may be maximising the time spent in enforced inactivity by carrying the infants together.

CHAPTER ONE

INTRODUCTION

Marmosets are tropical-zone arboreal animals, that rarely descend to the ground. They are omnivorous, feeding on fruit, leaves and gums as well as insects, small vertebrates and eggs. They prefer to live on the forest edge, and having a strictly diurnal habits use hollow trees or tangled vines for sleeping. The main predators of marmosets are Man, raptors, small cats and snakes. Marmosets travel around their territories carrying the infants, which is essential as they do not have nest sites in which to park the infants (Hershkovitz 1977). The aim of the research was to investigate the behavioural implications of carrying babies in the common marmoset, *Callithrix jacchus*. All family members, perform all forms of infant care with the exception of suckling. These activities include guarding, carrying, holding, comforting and infant socialisation (Whiten 1987). The family Callitrichidae, is unique amongst primates in its reproductive biology, social structure and care afforded by parents and older siblings to the infants.

This chapter will examine the group structure found in the callitrichid group, and specifically in marmosets, (See Table 1.1 for classification table). The reproductive strategy of marmosets will be described, in relation to reproduction in primates in general. The possible evolution of these traits will be discussed, and the selective advantages of caring for infants. The caregiving behaviour in primates in general will be compared with the way in which infants are cared for in New World monkeys and marmosets in particular. Finally, the place of this study within the context of the literature will be discussed.

Table 1.1

Classification of the suborder Platyrrhini.
(Smuts et al. 1987)

Suborder	
Infraorder	
Superfamily	
Family	
Subfamily	
Anthropoidea	Monkeys and Apes
Platyrrhini	New World Monkeys
Ceboloidea	
Callimiconidae	Goeldi's monkey
Callitrichidae	Marmosets and tamarins
Cebidae	
Alouattinae	Howler monkeys
Atelinae	Spider monkeys and woolly monkeys
Cebinae	Capuchins and squirrel monkeys
Pitheciinae	Owl monkeys, titi monkeys, uakaris, and sakis

1.1 The social and mating system.

In her discussion of monogamy, Kleiman (1977) proposed that the marmosets were obligately monogamous. She defines monogamy as the formation of a pair-bond that will exhibit mating exclusivity, when a male and female form a pair-bond for varying intervals of time, from a mating season to a life-time. This definition has, however, to be validated in the majority of species in the field. For this reason, monogamy is recognised in the field by a set of less strict rules including, close proximity of a pair both during and after reproduction. Normally only one pair in an extended family group breeds. The callitrichids, with their distinct reproductive biology are monogamous which enables the breeding female to have relatives to help her to raise the twin infants (Kleiman 1977). Kleiman (1985) states that paternal care may be correlated with monogamy or perhaps polyandry, and with small group size. There is evidence that the number of young surviving in the group is closely correlated with the number of adult males in the group (Sussman & Kinzey 1984). Group living may lead to decreased risk of predation, and the male, by guarding and defending his offspring, would be increasing his reproductive success.

Several authors (Kurland & Gaulin 1984; Vogt 1984; Kleiman 1977) are of the opinion that the evolution of monogamy may be influenced by ecological constraints. Clutton-Brock & Harvey (1978) and Pook (1984) agree that due to the highly specialised feeding and breeding patterns of the Callitrichidae, the home range will be related to the type of diet. For example Terborgh & Stern (1987) have shown in the saddleback tamarin (*Saguinus fuscicollis*) that territory size depends upon the amount of food available. Even if the distribution of the resources were such to allow the male to be polygamous, monogamy may be selected when the offspring are cared for. Not all monogamous

males carry their infants, but tend to do so if the infants are still dependent when large relative to the size of the female, and where there is no nest.

Vogel (1965) and Mitchell & Brandt (1972) proposed kin- selection to explain the maintenance of a monogamous group structure. Pook (1978) postulated that in evolutionary terms, the callitrichids may have already lived in a monogamous family group, and it was within this structure that twinning may have arisen. Vogt (1984) suggested that the presence of monogamy would promote paternal care of young as the male can be certain of paternity. However, Werren et al. (1980) concluded that certainty of paternity is not the only reason for the evolution of paternal care, but may be a contributory factor. Species such as Goeldi's marmoset (*Callimico*), Titi monkeys (*Callicebus*) and Owl monkeys (*Aotus*) that are much larger, are monogamous and exhibit biparental care. McGinnis & McGinnis (1978) also agree that paternal care is found in arboreal and small monogamous social units. Monogamy and biparental care lead to strong group cohesion, which is essential to ensure that the infants are not left behind when the family moves about the territory in search of food and sleeping sites.

Previous ideas based on knowledge to date about the callitrichids, suggested that they were primitive, monogamous and territorial (Sussman & Kinzey 1984). Recent field studies have put forward new ideas to explain the social system seen in the Callitrichidae in the wild (Garber et al. 1984; Sussman & Kinzey 1984; Terborgh & Goldizen 1985; Goldizen 1987 & 1988; Sussman & Garber 1987; Scanlon et al. 1988). These studies have shown that they have a specialised ecological role, and may not be exclusively monogamous. Sussman and Kinzey (1984) state that the family shows a "suite of characteristics that are unique among living primates". Field research shows that the preferred description of

the social system is one of a 'communal breeding system', with frequent migrations into and out of the group (Sussman & Garber 1987; Scanlon et al. 1988). A 'communal breeding system' is one in which the the mature offspring remain with their parents, but there may also be unrelated migrants within the group. The female may also engage in promiscuous matings with any of the mature males in the group. This would be described as monogamy with facultative polyandry (Sussman & Garber 1987).

Terborgh and Goldizen (1985) have shown that for a greater proportion of the time in *Saguinus fuscicollis*, there may be more than one breeding male present in the group. Although this may be the case, it does not negate the fact that in general there is only one reproducing pair and the extrafamilial members of the group raise their infants. Matings have been seen by more than one male in the group, and Terborgh & Goldizen (1985) report that non-mating males show no aggression towards mating males. There is also some evidence from the captive studies of marmosets that females would mate with more than one male if the opportunity arose (Rothe 1975; Abbott & Hearn 1978), although only one female produces young at any one time. Scanlon et al. (1988) presented evidence to show that some wild marmoset groups include more than one breeding female at a time. Terborgh & Goldizen (1985) and Scanlon et al. (1988) postulate that the dominance status of the female is fairly loose and may change quite frequently. There is no evidence yet that there is any form of inhibition of the capacity of all males in the group to mate, as seen in young subordinate females (Abbott 1984). In the wild, group size of the families is fairly stable, but the composition of the groups is constantly changing (Dawson 1977; Scanlon et al. 1988).

Goldizen (1987) proposed that the mating system may be dependent upon the

circumstances the family groups find themselves in. In her study of *Saguinus fuscicollis*, Goldizen has shown that there may be all types of mating behaviour occurring simultaneously within the same area. The group remained monogamous if there were related non-reproductive helpers available to help rear the infants. In the situation where there are no older offspring to help, the breeding pair may allow other males to enter the group and mate. If each male has had the opportunity to mate with the female, they remain to help raise the offspring. Lone pairs have not been seen to breed successfully in the wild. Cooperative polyandry is therefore a very complex phenomenon. Although it seems likely that the callitrichids may be living in a flexible 'communal breeding system', the arguments proposed to explain the presence of monogamy still hold.

1.2 Reproduction in the Callitrichidae.

Much attention has been paid to the unusual reproductive biology of the common marmoset; (Abbott & Hearn 1978; Lunn & McNeilly 1982; French 1983; Hearn 1983; Lunn 1983; Chambers & Hearn 1985; Moore et al. 1985). In captivity, females produce up to two litters per year, normally twins, and are simultaneously pregnant and lactating for most of their breeding lives. Once the female has given birth, the reproductive cycle resumes immediately (McNeilly et al. 1981; Hearn et al. 1986; Torii 1987). The ovarian cycle is approximately twenty eight days in duration (McNeilly et al. 1981; Hearn et al. 1986; Torii 1987). Ovulation occurs within ten days post-partum with the first lutenising hormone (LH) surge occurring 9-10 days post-parturition (Torii 1987). The first ovulation may lead to pregnancy if mating occurs, with a gestation period of approximately 144 days (Hearn et al. 1986). Implantation usually occurs 10-12 days after fertilization (Moore et al. 1985; Hearn 1986), much later than other primates. The callitrichids are unique among simians in producing

heterozygous twin, triplet and occasionally quadruplet offspring.

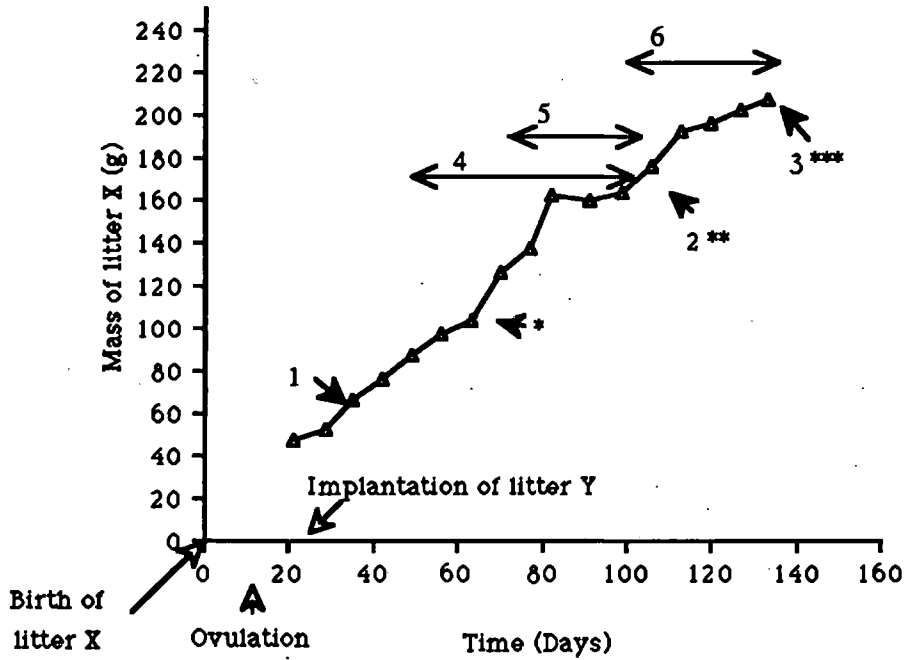
No change is observed in the body mass of the mother in the first thirteen weeks of pregnancy, but subsequently weight increase is proportional to the number of young *in utero*. The embryo remains at a constant length of 1 cm for the first 10 weeks of pregnancy, slowly increasing to 4 cm by the thirteenth week. At this point, the foetus grows very rapidly reaching the 8 cm length (28 g) usually found in infants at parturition (Chambers & Hearn 1985). Individual offspring weight decreases as the litter size increases (Lunn 1983), but these size differences disappear by maturity, with infants of single or multiple births having similar weights (Hershkovitz 1977). Fig. 1.1 is a summary of the changes that occur during a second pregnancy. (Data collected from the animals used in the study, for the rate of growth of infants and mothers post-partum are found in Appendix 1.)

The infants may suckle for up to 100 days although they start to be weaned at 3 weeks, (Lunn & McNeilly 1982). McNeilly *et al.* (1981) have suggested that, as there is a relatively long gestation period, with the infants being well-developed at birth, there is no need for an extended, lactationally induced, post-partum delay in ovulation. It has been shown that the high prolactin levels that occur after birth, and which are proportional to the number of infants sucking, have no effect on the female's ability to resume the oestrous cycle and become pregnant again (Torii 1987). In most mammals, these high levels of prolactin inhibit conception. It has not been clearly established why marmosets are exceptional.

The reproductive strategy of marmosets places enormous demands upon the mother, firstly by being simultaneously pregnant and lactating (Ingram 1975a), and secondly by supporting two infants rather than one (Redican & Taub 1981).

Either or both of these demands may favour group carrying of the infants, and a mating system whereby the male remains in the group and helps raise the infants. Ford (1980) and Pook (1978) proposed that twinning promoted the form of caregiving observed in these animals, with all members of the group helping to carry the infants. As French (1983) pointed out the energetic costs of reproduction and lactation are high. Marmoset milk has a very high protein content, about five times the protein content of human milk (Wright 1984), and would therefore be energetically costly to produce. Prentice & Prentice (1988) have postulated that the metabolic stress placed on the human mother is spread over a long period of time, as the foetus develops very slowly. Marmoset mothers have evolved ways to compensate for the heavy burden placed on them.

Fig 1.1 Body mass of litter X (n = 18), whilst female is pregnant with litter Y.



LEGEND:

1. Commence weaning of X
2. Female finishes suckling X
3. Birth of Y, (Day 144)
4. From day 40 infants can survive without mother, but continue to suckle to day 100
5. Foetuses of litter Y develop 1 cm - 4 cm
6. Foetuses of litter Y double in length 4 cm - 8 cm; female has least carrying role, and is no longer suckling infants X
- *. Day 70 crown-rump length of foetus of litter Y 1 cm
- **.. Day 100 crown-rump length of foetus of litter Y 4 cm
- ***. Day 144 crown-rump length of foetus of litter Y 8 cm.

1.3 Evolution of these traits

There is much debate over the phenomenon of twinning found in the family Callitrichidae. The debate centres around the occurrence of twinning in this family, and whether or not it is a primitive or derived character. Leutenegger (1973) argued that it is a derived character, selected as a response to dwarfism, where the adults became increasingly smaller. The general trend among mammals is for small adult body size to be associated with relatively high maternal investment in a single litter, so that smaller species have higher relative litter weights (Leutenegger 1977). Leutenegger proposed that callitrichids evolved from larger, singleton-producing ancestors. In primates, the relative size of the offspring is constrained by the width of the birth canal. The maximum recorded relative maternal-foetal weight for singleton births is 14% in *Saimiri*, where the females often experience severe birth difficulties due to the size of the birth canal in relation to the size of the neonate's head. Callitrichids have relatively large litters (twins at term account for as much as 24% of the mother's weight in *Cebuella pygmaea* (Leutenegger 1977)), and Leutenegger proposed that increased reproductive investment has been achieved by the production of two small infants rather than one large one. The regular occurrence of multiple births in small-sized species may have been selected because it promotes successful delivery of the foetuses. In support of this theory, Leutenegger cites the single pair of nipples and unicornuate uterus, both of which are normally associated with singleton birth, and are present in callitrichids. Leutenegger proposed that if ancestral callitrichids had been the same size or smaller than the modern day species, then twinning could be explained as the retention of a primitive trait with no monovular stage. This scenario however would not account for the features associated with single births. He concludes that gradual dwarfism led to relatively larger foetal size

and twinning.

Hershkovitz (1977) saw Leutenegger's argument as too complex, claiming that dwarfism would be accompanied by either a decrease in relative offspring weight, or an increase in birth canal size in order to compensate for an increasing relative litter weight as body size decreased. There is a trend towards increasing offspring size and decrease in litter number, accompanied by a corresponding increase in adult body size among primates. The argument that uterus type reflects the number of fetuses is invalid as it is not always correlated with litter size. Some marmoset species have primitive bicornuate uteri (Hampton 1975, cited in Hershkovitz 1977) usually found in animals that produce multiple litters.

It seems appropriate now to look at the costs and benefits of parental care incurred by all members of the family. Firstly by examining the behaviour of the female, then the male, older siblings and lastly the infants. The benefits of cooperative caregiving to the female are obvious, whilst other members of the family take the infants, the female is left able to forage and move about freely (Redican & Taub 1981; Wright 1984; McKenna 1987). Thus her energy expenditure is minimised or reduced, and hence she is able to reach the best resources unhindered. Several studies (Jolly 1984 and Richard & Nicoll 1987; pers. comm.) have shown that the female becomes dominant in foraging and so has access to the best resources, often at the expense of the male. This situation helps the female to meet the strenuous physical burden placed upon her by simultaneous pregnancy and lactation. The costs to the female in allowing alloparenting are these: the infants may be treated roughly by other members of the troupe or even kidnapped, and she may have trouble retrieving them (Kohda

1985; McKenna 1987).

The benefits for the male are that he is increasing his own reproductive success by promoting successful raising of the infants (Wright 1984), and the female is able to produce more of his offspring. Studies have also shown that there may be a correlation between the number of males in the group and the young surviving (Sussman & Garber 1987). As they are a monogamous pair, the male is assured of the offsprings' paternity. There are costs to the male in giving care to the infants. The relative costs of most forms of locomotion in a smaller animal are proportionally greater than in larger species, therefore, nutritional requirements, per kilogram, are higher in animals with a smaller body-size (Clutton-Brock & Harvey 1978). As body mass of the infants is high relative to that of the male and they are growing fast, the costs of locomotion and carrying the infant are very high. Whiten (1987) has shown that in some cases there may be an increase of up to 17% in locomotor costs whilst carrying infants. There may also be decreased foraging efficiency since the female may get to the resources first (Wright 1984). Protection of infants may also be very energetically demanding.

As it may not always be possible to leave the family, the adolescents stay and help to care for their younger siblings, which raises their own reproductive success when they leave the group to breed. The benefits to the older siblings and other offspring found in the family group are the opportunity to learn valuable parenting skills, which later enable them to rear their own offspring successfully (Hunt et al. 1978; Tardiff et al. 1984; Cleveland & Snowdon 1984). As well as delaying their own reproduction, the cost incurred to the older siblings is a decreased level of parenting because the parents are no longer able

to invest exclusively in them, as they have their newborn infants to care for (Trivers 1974; 1985). The breeding pair may also have an inhibitory effect on the reproduction of the older offspring in the family group, although this mechanism is not fully understood (Abbott & Hearn 1978).

The presumed benefits afforded the infants are an increased chance of survival, and, since there are so many related caregivers, the infants may be able to garner more care than they would otherwise receive. Although the mother frequently rejects the infants after the first few weeks, the other group members care for them. Since marmosets are arboreal, there may be a selective advantage to carrying the infants in time of danger even when they are nutritionally independent. Locke-Haydon (1984c) believed that infants not carried by other family members would not be able to keep up with the troupe, and as a result would not survive. The other members of the family are also important in the socialization process of the infants (Ingram 1977; Mendoza & Mason 1986). Some of the costs incurred by the infants include the possibility that they may be badly treated by the inexperienced siblings. The infants are in no way aided to hold onto the pelage of the caregiver, although carers may approach very young infants and attempt to pick them up (Rothe 1975; Stevenson 1976).

1.4 Comparative caregiving.

The New World monkeys have evolved from New World prosimians, independently of the Old World monkeys, since the Eocene. They are all strictly arboreal and there is only one nocturnal genus. The Old World monkeys are found in Asia, Africa and Europe, and are sometimes semi-terrestrial. There are two main theories that explain the caregiving and social systems found in the callitrichids. Briefly, the first is that monogamy (or the facultatively

polyandrous family groups found in the callitrichids) leads to a greater degree of certainty of paternity, and promotes the evolution of paternal care for the infants, which may be linked to arboreality. The second is the small body size of these primates, and the phenomenon of twin births as the normal litter size. To enable the female to cope with being burdened in this way, the male and other members of the family group have become important in the care of the infants from an early age. From this situation, three predictions arise about the care system of the callitrichids. The first is that the degree of paternal care is a response to the type of social group found in a particular species. The second is that small adult body size may be linked with paternal care. The third prediction suggests that arboreality necessitates the carrying of the infants to ensure that they are protected and can travel around the territory. However, it should also be noted that small adult body size may also be associated with an arboreal life style since arboreality may impose an upper limit on adult size. By examining other primate groups it will be possible to assess the validity of these predictions.

Vogt (1984) and Nowak & Paradiso (1983), have reviewed the parental care systems of the prosimians. These animals are generally solitary or monogamous, and arboreal. Some of the small-bodied species have multiple births, but the degree of paternal care of any kind is almost negligible. The infants of many species, such as loris (*Nycticebus coucang*), potto (*Perodictus potto*) and the galagos are left, 'parked' hanging onto branches at night whilst the female is foraging. The infants are returned to the nest during the day. Some paternal care has been observed in Sifakas (*Propithecus*), where the male does carry the infants, but to a much lesser extent than the female. The males form pair-bonds with the females within a large group (Whiten 1987).

Amongst the monogamous primates, the male partakes in caregiving activity, as is the case in the marmosets and tamarins. The only other monogamous and arboreal primates are the gibbons (*Hylobates*) and siamangs (*Symphalangus*). These are the smallest of the apes, and they hold territories. They are much larger than the Callitrichidae, and, typical of larger primates, have singleton births. They also have longer gestation periods and interbirth intervals. The role of the male in infant care, although important, is not so important as that of the male callitrichid. It should be borne in mind that these Old World primates have evolved separately from those found in the New World, and as such may have adapted in different ways. The male gibbon has been seen to groom, inspect and carry the infant for a greater part of the day, while the male siamang cares for the infant after the first year until it is weaned at three years of age. As with the prosimians, the infants are carried around the territory by the parents (Nowak & Paradiso 1983).

The other primates remaining to be examined are the Old World monkeys. Those species that are generally terrestrial are found in larger groups (Jolly 1972). The arboreal species tend to be larger in size and live in extended multimale/multifemale groups. The adults tend to have a much larger body size than either the prosimians or callitrichids. The females generally give birth to singleton infants, and only rarely have twins (Schaub 1987). 'Barbary' macaques (*Macaca sylvanus*) live in 'harem' groups with one male and many females, or in multimale/multifemale groups. The degree of certainty of paternity is greater in the 'harem' species than in the promiscuous multimale/multifemale groups, but less than in monogamous pairs. It seems plausible to predict that the degree of paternal care elicited by the infants in such groups is less than that from the monogamous pairs, but greater than that from the promiscuous males.

The 'Barbary' macaque males establish strong relationships with infants within their group, although no preference is shown for closely related infants. This is unusual since these macaques live in promiscuous groups. The male care is neither as frequent or as constant as that found in the monogamous species described earlier. However, the species occurs in very harsh habitats which may explain why there is this level of paternal care (Whiten 1987). There may be variable quantities of paternal interactions with infants, in the promiscuous groups. Male caretaking has been observed in several of the macaque species. Kuester & Paul (1986) have found that male *M. sylvana* established strong relationships within their group, although no preference was shown for closely related infants. Mitchell & Brandt (1972) in a review of paternal behaviour in primates, mentioned that rhesus macaque (*M. mulatta*) males sometimes adopt motherless infants. Itani (1959) found that in Japanese macaques (*M. fuscata*), the dominant or subdominant males would care for infants up to the age of two years. Brandt et al. (1970) have shown that the younger males are more likely to engage in caregiving behaviour than older, more mature males. Busse & Gordon (1984) found a similar situation among the black mangabey (*Cercocebus aterrimus*) males. The females of this species are very possessive of their infants and will not allow young infants to interact with males. Adult male chimpanzees (*Pan troglodytes*) rarely interact with the infants and Redican & Taub (1981) postulate that this situation is due to the promiscuous nature of the group. They also discuss the male-infant interactions found in the cynocephalus baboons. By the age of five to six months, the females' caring role of the infant has decreased to a negligible level. The males, who have been interacting with the infants since the first month of life, now become important in the role of protecting the infants and mediating in squabbles that may occur.

Another type of social organisation considered by Redican & Taub (1981), are the one-male/multifemale groups. These are groups in which there are many females and their offspring and there is only a single mature male present. Any additional males are excluded and live alone or in 'batchelor' groups. There are relatively few primate species of this type, among them hamadryas baboons (*Papio hamadryas*), gorillas (*Gorilla*), gelada monkeys (*Theropithecus gelada*), and langurs (*Presbytis*). Redican & Taub (1981) described the role of the male in caring for the infants in the first three species mentioned. In the hamadryas baboon, the males frequently carry the infants on their backs whilst the groups are travelling, and the infants may sleep with the male at night. In the case of the gelada monkey, a young male of the peripheral 'batchelor' group carries the infant ventrally or dorsally, and also plays with the infants until he becomes leader of his own harem. Male gorillas have been observed to care for orphaned infants, and groom infants to a greater extent than a mother would. In patas monkeys (*Erythrocebus patas*) (Chism 1986) and langurs (Dolhionow & Murphy 1982), the males play a very minor role in the care of infants. The male patas monkeys defend the territory, the females and their infants.

To summarise, the Old World primates being generally terrestrial and having a larger adult body size, exhibit paternal care to a lesser degree than the monogamous species described. They also tend to live in larger groups in which the dominant males can defend larger territories. The arboreal species also tend to live in larger, more promiscuous groups, in which little paternal care occurs. In certain circumstances the males may be observed to interact quite closely with infants that may or may not be related to them.

1.5 Care-giving in the Callitrichidae.

Details of care-giving behaviour in *Callithrix jacchus* are well documented (Epple 1970; Rothe 1975; Box 1975b, 1977; Ingram 1975a, 1977; Stevenson 1976; Locke-Haydon & Chalmers 1983; Locke-Haydon 1984a; Chalmers & Locke-Haydon 1985; Engel 1985; Arruda et al. 1986). It should be noted however that there is very little field data for many of these species, with much of the information coming only from laboratory data. The New World primates fall into two groups with regard to infant care. The first category includes *Callithrix*, *Callimico goeldii*, and lion tamarin (*Leontopithecus rosalia*) (Cleveland & Snowdon 1984), pygmy marmoset (*Cebuella pygmaea*) (Wamboldt et al. 1988), and cottontop tamarin (*Saguinus oedipus*) (Tardiff et al. 1984; Kleiman 1977), where the mother may be the primary caregiver in the first week after birth. The second category, in which the father and older brothers may be primary caregiver in the first weeks of the infants' life, includes all the tamarins of the genera *Saguinus* (Cleveland & Snowdon 1984), *Callicebus* (Wright 1984; Mendoza & Mason 1986) and *Aotus* (Wright 1984).

Observations of captive animals have shown that parturition usually occurs late at night or in the early hours of the morning (Stevenson 1976; HersHKovitz 1977). Immediately the infant is born it must cling to the fur of the mother and move unaided across the mother's body, (Rothe 1975; Stevenson 1976). The infant orientates itself with its head upwards, and moves to the usual rest position across the caregiver's shoulders (Kohda 1985). In contrast to the Old World primates in which the infant clings to the belly of the mother, marmoset infants cling to the shoulder of the caregiver, and are only found on the ventral surface of the female during suckling. *Aotus* infants ride on the groin of the female (Kohda 1985), but are found on the back of the male (Welker & Schaffer-

Witt 1987). The infants of the Old World primates are held and supported as the mother is moving (Kohda 1985), but New World primates never support the infants or direct them, even whilst the adult is moving. The marmoset infant is not held, infants crawl rapidly across the body of the care-giver, and spontaneously change care-givers if they are in close proximity. Old World monkey infants are passed from one carer to another (Kohda 1985). Occasionally the caregiver takes the infant during a transfer and ano-genitally grooms the infant, which stimulates urination and defaecation. The infant then continues to climb to a resting position on the shoulder. In *Callithrix jacchus* in contrast, the newly born infant lies across the neck of the caregiver in a transverse position. Infants of other species such as *Saimiri* and *Aotus* are carried longitudinally along the back of the caregiver (Kohda 1985). The family members are strongly attracted to the infants, which elicit caregiving behaviour. The male *Callithrix jacchus* has been observed to carry the infants within an hour of their birth, while still wet, and all adult family members may carry the infants from the first day (Stevenson 1976).

There is general agreement that from birth to about three weeks of age the infants are constantly carried by the members of the family (Epple 1970; Box 1975b; Anzenberger pers. comm.; pers. obs.). During the first week the mother may be the primary caregiver but after the second week, the father and older siblings becomes the principal carriers (Ingram 1977; Arruda et al. 1986) and continues in this role for several weeks. By the sixth week, carrying by any of the caregivers has fallen to a minimum (Locke-Haydon & Chalmers 1983). As the proportion of time being carried by all caregivers falls, so the amount of time spent on the mother rises proportionally, with the decline of care offered by the male and older siblings. The role of the mother is important as she still suckles the infants. When the juveniles are too large to be carried, they spend a greater

amount of time in contact with their mother purely for feeding. The male and older siblings are involved in play behaviour, an activity in which the mother rarely or never participates. Play has an important function in the increasing socialisation of the infants, who do not have a large family group, as found in the Old World primates to interact with. Male involvement is especially important if there are no siblings present. Although carrying decreases rapidly after the sixth week, the infants will turn to the caregivers when threatened. It is generally the male who carries the infants since the mother is normally pregnant again by this time, and unable to retreat from danger successfully to safety with the infants (Wright 1984; Wamboldt et al. 1988).

The older siblings also help to carry the infants, although the care given can be variable in quality. Caregiving by siblings may be the result of their response to a lack of unoccupied territorial space or of suitable partners, forcing them to remain in their natal group until they can establish their own pairings. Kin-selection theory (Hamilton 1964) predicts that if siblings cannot rear their own offspring, they may maximise their own inclusive fitness by helping to rear younger siblings. It may also be to the advantage of the siblings to help carry the infants, since the experience may improve their parenting skill and so enable them to raise their own offspring more successfully. This would be a system of altruism as predicted by kin-selection theory (Hamilton 1964), as the infants would in turn be able to raise the offspring of their older relations (Terborgh & Goldizen 1985). This effect appears to be more important for the siblings of the genus *Saguinus* than marmosets (Tardiff et al. 1984). With increased number of siblings in the family group, the level of care provided by the adults, and the male in particular, decreases (Box 1975a).

Engel (1985) and Ingram (1977) have proposed that due to the whole family helping to raise the infants, the weaning process is less traumatic for the infants than in Old World primates. They also propose that these infants are better able to withstand changes in their environment, as they will be more tolerant of variable conditions than infants raised exclusively by one caregiver. They also propose that the adults will be tolerant of 'help' from the siblings which assists the female who will be enduring the high energy demands of lactation and pregnancy. The presence of older siblings leads to a reduction in the amount of carrying that the adults have to undertake, especially the male (Box 1975a).

Independence in the infants is promoted, primarily by the respective caregivers (Ingram 1975 and Locke-Haydon & Chalmers 1983), as predicted by parent-infant conflict (Trivers 1974). Locke-Haydon & Chalmers (1983) and Locke-Haydon (1984b) reported that the amount of time spent on a caregiver is determined by the relative rejection rate shown by the carriers toward the infants.

1.6 Research resumé.

Reproductive female callitrichids are simultaneously pregnant and lactating, which imposes a heavy physiological burden. The social system is such that all members of the family help to carry the twin infants (Box 1977; Locke-Haydon 1983; 1984c and Locke-Haydon & Chalmers 1983). Having established these facts I wanted to look at the behavioural effects that carrying infants may have upon the caregivers, as this aspect of infant caregiving has not yet been studied.

The aim of the research was to investigate the behavioural strategies used by the family to cope with the huge demands that are placed upon the female. Given that

only the female is able to suckle the infants, she must carry the infants for at least part of the day until the infants are weaned. The effects of carrying infants, upon the behaviour of the other members of the family were also studied. Siblings that remain in the family, and help to raise the infants, remain reproductively inactive (Abbott & Hearn 1978), although they are sexually mature by thirteen to fourteen months. The mechanism by which the siblings are reproductively inhibited is not fully understood although these may be social and hormonal, Abbott (1984) has suggested that there may be a chemical which triggers the anovulatory state of the daughters in the family. Tardiff *et al.* (1984), found that infant mortality rate was increased in pairs that had had no prior experience in infant caring in *S. oedipus*, but found that rearing experience was beneficial, although not essential for *Callithrix jacchus*.

The mobility of the care-givers in relation to infant carrying was analysed. Goldizen (1987) observed that the caregivers carry their infants to a greater extent whilst they are resting. Some studies, for example Box (1975b) and Goldizen (1987), have shown that the caregivers may behave differently when carrying infants. For example mothers did not carry infants, and even rejected infants' approaches, whilst eating. Johnson (1986), suggested that the female rhesus macaque may carry the infant whilst moving to minimise her energetic costs. The female may incur extra costs by trying to force the infant to ride on another adult, so that, whilst she is the primary source of food, it would be energetically more economical for her to carry the infant. This would apply to marmoset caregivers who have to carry the infants around the territory. If one caregiver had both infants other group members would be free to forage.

Data were collected in such a way that it would be possible to assess whether or

not the female, and other carriers, tended to carry the infants simultaneously or sequentially, or perhaps to have no load at all.

The lengths and frequency of carrying bouts were recorded. In this way it would be possible to assess whether there were differences between carrying bouts in which one or two infants were carried.

The rate of movement of the infants onto and off the caregivers was also examined in detail in an attempt to find out whether or not the bouts of infant carrying were adult or infant initiated.

CHAPTER TWO

COLONY MAINTENANCE AND RESEARCH METHODS.

COLONY MAINTENANCE.

2.1 Housing.

The marmoset colony is housed in four rooms within the Animal Unit of the Science Faculty, at the Open University, (Locke-Haydon 1983).

Room 1 is 3.6 m long x 3.8 m wide x 2.3 m high,

Room 2 is 3.5 m x 3.8 m x 2.3 m,

Room 3 is 5.4 m x 3.5 m x 2.3 m,

Room 4 is 5.8 m x 5.1 m x 2.3 m, (See Fig. 2.1 for floor plan of the rooms used in the study). Rooms 1 and 2 have 1.2 m x 0.5 m one-way, smoked glass observation windows. Room 3 has a much smaller ante-room with two smaller windows, one smoked, the other plain. The smoked window is set in the inner door that leads into the room that houses the animals. This room was probably not originally designed for observational use and is certainly not comfortable for extended periods of observation. Room 4 is the largest of the rooms that houses the animals and was recently converted from use as a cold room.

There is an observation cabin built into the centre of the room which has one-way windows that can be blacked out. The observer is housed in the ante-room in order that the families remain undisturbed and the behaviours observed (and data collected) are as natural as possible. The one-way windows work on differential light levels between the animal rooms and in the observation ante-

rooms on the other side of the glass. To aid efficient use of the windows, there are dimmer switches in the ante-rooms, and blinds are pulled down over the windows when not in use. The darkened ante-rooms act as separation chambers to keep the monkey rooms apart from the rest of the animal unit. This arrangement cuts down on the level of disturbance to the animals, so that the animals are housed in as constant conditions as possible. Each of the ante-rooms is equipped with a micro-computer system for recording and analysing the observation sessions.

The rooms, which have no external source of lighting, have lighting provided from two light sources each of 200 W, mounted on the ceiling. In addition there are *Truelight* 65 W fluorescent strips placed above the smoked glass windows. These strip-lights provide light which is very nearly equivalent to natural light. (Duro-Lite Int., New Jersey, U.S.A.).

All the light sources are controlled by time switches which were on from 6.30 a.m. to 6.30 p.m. to give twelve hours of artificial daylight. The first and last 30 minutes of the light schedule are simulated dawn and dusk periods of twilight so that the rooms are not plunged into darkness or light, which can cause the animals to fall from perches and be injured (Kingston 1969). However, in Room 4, the most recently converted room, there are no twilight periods and to date there have been no cases of animals being injured as a result of the abrupt light changes.

The rooms are held at a constant temperature in the range 25 - 28°C, with the humidity set at 50 - 60% R.H. The heating is controlled via the air ventilation, with 18 air changes per hour. Air filtration is not highly efficient, with all the

rooms, except Room 3, being of positive pressure to the main corridor. Room 3 was a quarantine room, and had of necessity a negative air pressure to that of the main corridor. Negative air pressure causes air to be pulled into the room, so that all exhaled gases and any infectious particles cannot escape into the main air-flow. The main corridor air pressure is positive to the exterior of the unit.

Cages were made or modified by the Open University workshops. Dimensions of an average cage are 1.8 m high x 0.88 m wide x 0.75 m deep. The wire netting used is 2.5 cm mesh, the sheets of which are held together in an iron frame.

There is a removable tray at the base filled with sawdust for collection of droppings and waste food. Each cage has a metal nest-box measuring 30 x 19 x 20 cm. The box rests on a shelf in the cage, and has a sliding door on the side to facilitate capture and transfer of the animals. The cage also contains wooden perches and swings. In the last year gum sticks were introduced for gnawing (McGrew et al. 1986), and occasionally foraging boxes filled with coarse wood shavings were put in the cage to stimulate varied activity. There were metal sheets attached to the sides of the cages so that the animals can hear but not see the other families housed in the same room. The absence of visual contact helped to cut down on the disruption of normal social interaction by territorial behaviour.

The floor-tray sawdust was changed and the rooms and cages cleaned once a week. The nest-boxes were removed and cleaned every one to two months, at a different time to normal room cleaning, to allow some of the family scent to remain at all times. The food bowls were cleaned daily and water bottles weekly. The floors of all the rooms were hosed down daily to help keep the humidity high, and overall smell in the rooms at a tolerable level for those members of staff that had to work

in them on a daily basis.

Each cage held one family group made up of the adult pair, and up to two sets of offspring. When the next set of infants are born into the family the eldest siblings are removed to maintain the family composition and help to reduce overcrowding.

2.2 Feeding and health.

The diet fed to the marmosets in the colony was developed from that given by Stevenson (1976), and consisted of the following components: 40 g of mash per animal, made up of CPDX New World Primate Diet, (Labsure Animal Diets, Christopher Hill Group Ltd., Agranon House, Castle St., Poole, Dorset), was given on Monday, Tuesday, Thursday and Friday of every week. In addition to the mash some meat was added, such as "Chum" canned dog food, (Pedigree Petfoods, Melton Mowbray, Leicestershire), for additional protein. The mash also contained either South American Monkey Pellets or Jelly, (S.D.S. Witham, Essex), for added vitamin supplements, together with 0.6 ml per cage of Abidec, a vitamin solution, (Warner Lambert Health Care, Eastleigh, Hamps.), and 0.5 ml of Corn Oil (containing linoleic acid) which helps to prevent and cure hair loss.

On the remaining days of the week the animals are given a standard fruit diet, which is chopped into pieces of a suitable size for the marmosets to pick up and hold, as they do not tend to take larger items (Kingston 1969). Trial and error was used to see how much each family would consume and these proportions were used on a regular basis thereafter. The diet consisted (in g per animal) of, 20 g each of banana, apple, pear, and meat, 15 g each of orange and tomato and one grape and peanut per animal, and one egg and a Farley's rusk were given per

family.

Water was supplied from bottles hung on the outside of the cage, which was continuously available, these bottles were refilled with fresh water daily. 100 ml/l of Cytaccon, a vitamin B12 solution, (Glaxo Labs. Ltd., Greenford, Middx.), was added to the drinking water once a week, per pair of adults. The solution may last up to two days after which fresh water was again freely available.

In addition, 50 ml of milk, made up from full cream milk powder, was given per family three times a week. Marmosets have a high vitamin D3 requirement because they are unable to synthesise it from provitamins in the skin, as there is no natural light in the animal unit, so 0.04 mg of vit D₃, (Rovimix Vitamin D3 Type 500W, Roche Products Ltd., Welwyn Garden City.), per cage was added to the milk. It was necessary to give vitamin D3 only, since platyrrhines use it effectively in the metabolism of calcium and phosphorus for bone formation. Since vitamin D2 is not utilised in this way, it was not necessary to add it to the diet.

A continuous supply of nutritious, vitamin-supplemented food is the most probable cause of the rising incidence of triplet births in captive colonies (Ingram 1975b; Pook 1976; Box & Hubrecht 1987). Although there were a very high proportion of multiple births with more than two infants being born, this colony has experienced very few obstetric problems.

There have been very few medical problems detected in the colony since its inception. In some cases, older females required caesarian sections. This necessitated hand-feeding of the infants as the mother did not lactate. An hereditary oesophageal constriction killed one adult male and his son. In both

cases the animals were about two years of age at time of death. Due to recent building work in and near to the animal unit there have been some spontaneous abortions, the ovarian cycling of a number of the females was severely disrupted and the birth rate fell. There have also been some liver and renal problems. As a result of lowered humidity at the time of building work, there were a few cases of quite severe ringtail.

2.3 Handling and hand-rearing.

The animals are handled firmly but cautiously wearing thick leather gloves. They were handled only for weighing and injecting with Modecate (Fluphenazine Decanoate; E.R. Squibb & Son Ltd., Middx.), for use in an experiment being conducted by Dr. Hubrecht. As I had to use animals also being used by Dr. Hubrecht, two of the families I observed had members that had been injected with Modecate, (see Table 2.1). The animals were placed in a small mesh cage 240 x 190 x 140 cm on a Mettler PK 16 electric balance. The infants were weighed on the day of birth, and then once a week until they are 20 weeks old. The mother was also weighed with the infants. The other members of the family were only weighed on days that they are the focal animals in observational sessions, (see methods section for full details). The adult animals were identified by necklaces with coloured discs attached. Blue discs were used for the males and red for females, each with an individual number. The infants and juveniles had the hair on their tails clipped, and occasionally had their ear-tufts dyed yellow with a hair dye. None of the handling and marking procedures appeared to have any affect on the natural behaviour of the animals.

In the event that triplets were born, the weakest infant generally died within three to five days. Should the infant be injured or suffering it was removed from

the cage and destroyed by an overdose of 1 ml of 60 mg/ml Sagatal anaesthetic, (Pentobarbital sodium, May and Baker Ltd., Dagenham Essex), injected intraperitoneally.

On occasions when the infants had to be hand-raised the following procedure adapted from Ingram (1975a) was followed. Initially four feeds a day were given, and these were gradually reduced to two feeds of milk and one of a water and vitamin supplement. After the first week, the infant was strong enough to fend for itself, although a close check was kept on its progress. This procedure was implemented on the first occasion that family 11a raised triplets, the smallest infant was given some supplementary feeding.

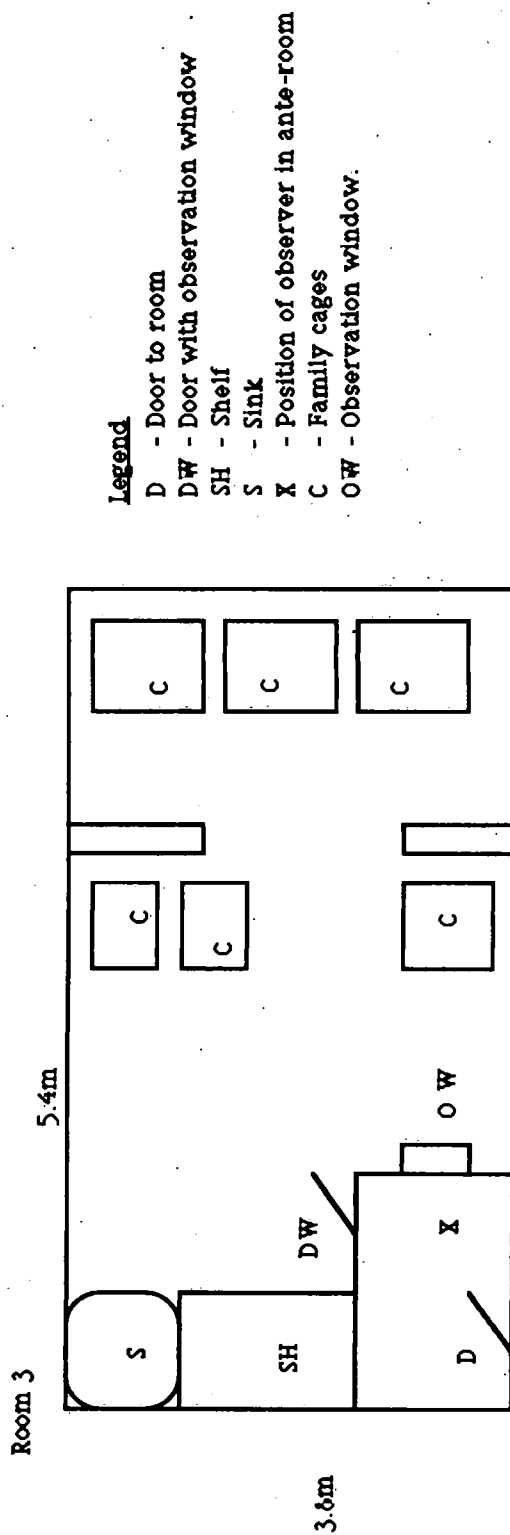
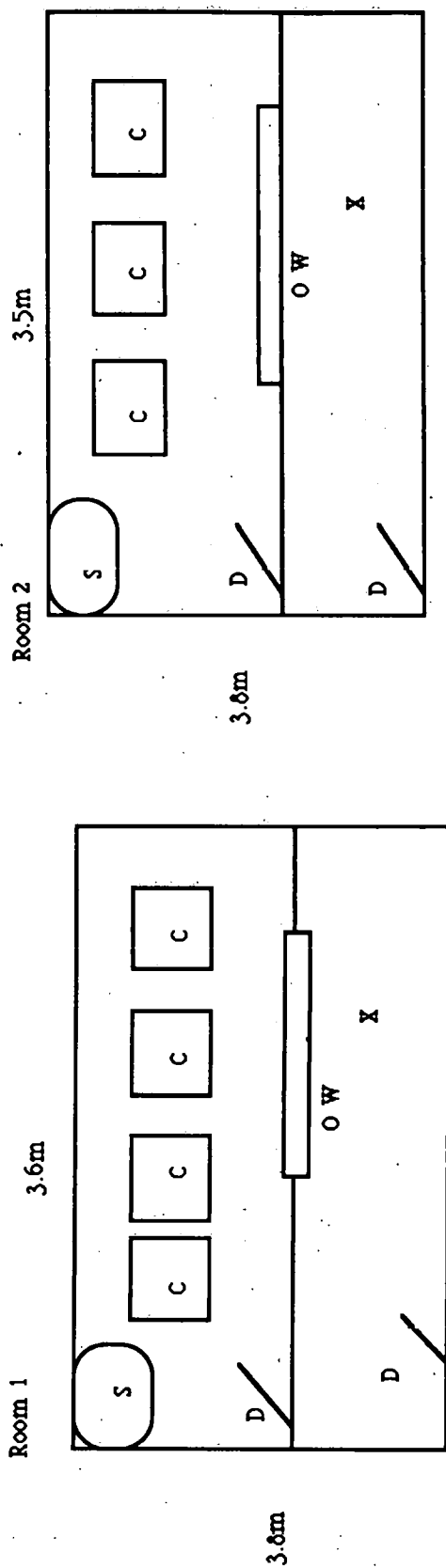
2.4 Colony composition and animals used.

The colony of marmoset monkeys, *Callithrix jacchus*, studied at the Open University was formed in 1978 from six adult pairs, all obtained from other colonies of captive animals. Five of the animals were born in captivity and the sixth, a male, was born in the wild. The reproductive adult pairs are housed in family groups of up to six animals. At present there are fourteen family groups varying in size from newly formed breeding pairs to those that have up to three litters of offspring. Most families raise twins, but there were exceptions; some had only singletons and one family spontaneously raised two successive sets of triplets.

Some families within the colony were used as part of another research project. These animals were injected with Modecate (E.R. Squibb & Son Ltd.). Modecate is a neuroleptic, fluphenazine decanoate, which was used to depress the social interactive behaviour of the animals. The drug, administered by intramuscular

injection, is a tranquilizer but not a sedative. The drug is believed to depress some components of the mesodiencephalic activating system which controls basal metabolism, body temperature, wakefulness, and hormonal balance. The site and mode of the action are not clearly understood (Locke-Haydon 1984b). The caregivers were made more passive and withdrawn. The drug treatment was expected to cause relationships to become less intense, and to be less controlled and dominated by the caregivers, who become more passive and tolerant (Locke-Haydon 1983). In many cases, there were no obvious changes in the behaviour of the caregivers towards the infants. Two families used in my study were a part of this research. In one case, all the caregivers were injected, in the other only the parents were treated.

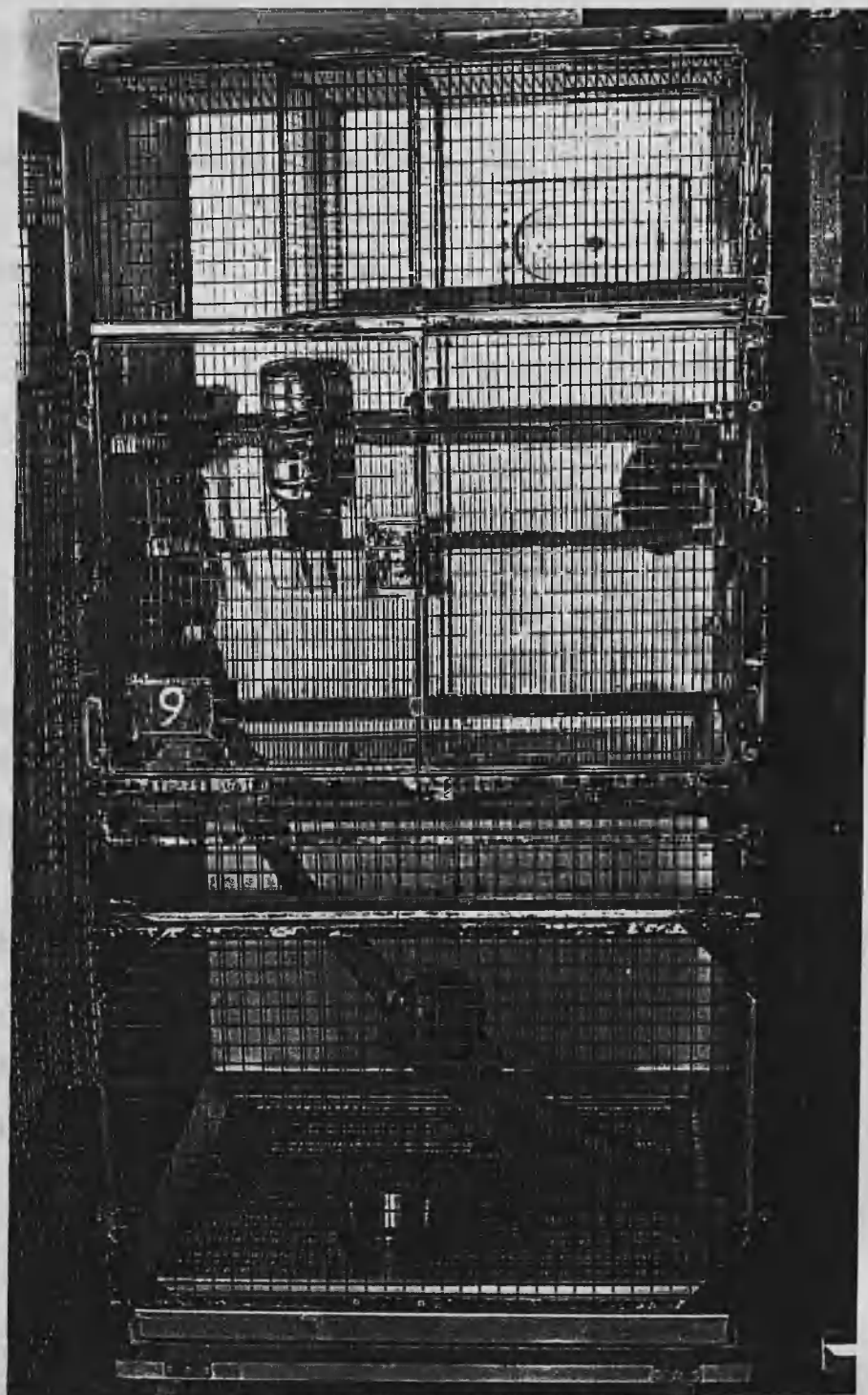
FIG. 2.1 FLOOR PLAN OF THE MARMOSET ROOMS USED IN THE STUDY.



Legend

- D - Door to room
- DW - Door with observation window
- SH - Shelf
- S - Sink
- X - Position of observer in ante-room
- C - Family cages
- OW - Observation window.

Fig. 2.2 Typical cage used to house a family of marmosets in the colony.



For the project I studied families comprising the adult pair, older siblings and the newborn infants. The siblings were always from the litter born before the set of infants to be studied. The data used were collected from a total of eight families. (See Table 2.1 for summary of families used in the study).

Table 2.1 Marmoset families used in this study.

Cage	No. of caregivers	No. of infants	Moderate used	Family size
1	4	2/1	No	6/5
3	4	2	No	6
4	4	2	Yes	6
8	4	2	No	6
8b	4	2	Yes	6
9	4	2	No	6
11a	4	3	No	7
11b	5	3	No	8

Cage 1- one infant died after three weeks, leaving a singleton for the second half of the experiment.

Cage 11a - triplet infants raised.

Cage 11b - triplet siblings and triplet newborn infants.

RESEARCH METHODS

This section describes the particular behaviours observed and recorded, method of data collection and organisation for presentation and analysis.

2.5 Behaviours observed.

The object of the project was to investigate the effects that carrying infants had on the behaviours of their caregivers. The behavioural categories used in the study are listed below.

2.5.1 Behaviour states:

A 'state' is defined as a behavioural category which lasts for a measurable time and which is delimited by the moment it begins and the time it ends.

Time on: The state recorded during my observation sessions was the amount of time spent on a caregiver by the infants, either simultaneously or individually.

'Time on simultaneously' is defined as the time from which the second infant climbs onto, or is picked up by, the caregiver until it climbs off, or is rubbed off by, the caregiver. 'Time on individually' is defined as the time spent on the caregiver, and may include carrying bouts in which the second infant has also been carried for a while in a simultaneous carrying bout. The infants may be carried in any position (dorsal, lateral, etc.) provided that, if the caregiver moves away, the infant moves with it. The infants cling onto the fur of the caregiver and are not held on by the caregivers themselves.

For the remainder of the results and discussion these states will be denoted

State 0 when the caregiver is not carrying any infants; State 1 when one infant is being carried, and State 2 when the caregiver is carrying two infants.

2.5.2 Behaviour events:

An 'event' is a behavioural occurrence for which a duration measurement is not taken. In most cases the events occur instantaneously, although a rub off attempt may take some time. It is the event that is of importance to this study, not how long it takes to complete.

Infant picked up: The initiation of a bout of 'time on' by a caregiver. The caregiver leans towards the infant, or approaches the infant, and the infant responds by clinging on to the caregiver. On occasion, the caregiver may grasp the infant with one or both hands.

Infant climbs on: A bout of 'time on' initiated by the infant. The infant crawls or climbs onto the caregiver without any assistance from the caregiver.

Infant climbs off: The termination of a bout of 'time on' by the infant. The infant crawls off the caregiver apparently of its own accord.

Infant rubbed off: The termination of a bout of 'time on' by the caregiver actively removing the infants from its body. The caregiver scrapes the infants off by rubbing it against the floor or the side of the cage; the caregivers may also attempt to push the infants off with their hands.

Infant rejected: A caregiver prevents the infant climbing on to it, or prevents it coming into contact with it, by pushing it away or keeping at a distance from the infant. The caregiver may also lunge or bite at the infant while making 'erh-erh' vocalisations (Stevenson & Poole 1976).

Activity levels: The level of activity was measured by recording the frequency with which the caregiver crosses horizontal and vertical midlines of the cage.

Horizontal grid cross: The focal animal moves across the midline of the cage, dividing the left half from the right. The caregiver may or may not be carrying one or both infants when it makes this move across the cage.

Vertical grid cross: The focal animal moves across the midline dividing the top half of the cage from the bottom half. It may or may not be carrying one or both infants as it moves across the cage.

2.6 Recording of observations.

2.6.1 Watching schedule

The method of observation used followed the 'focal-animal sampling technique' used by Altmann (1974). The method involved the continuous recording of the behaviour produced by, or directed to a single individual, designated the focal animal, for a predetermined length of time. This method is a good technique for the study of frequencies, durations and sequences of behaviours performed during the observation sessions. It also allows the data to be compared across subjects and ages, with the provision that all focal animals are observed for equal lengths of time and under comparable conditions. The data were entered directly into a computer (see section 2.6.2 for details of the use of the computer), and during the observation sessions, additional handwritten notes were made of the interactions between the animals other than the data collected on the computer. These notes included details of aggressive bouts and which

individual was carrying the infants when not being carried by the focal animal.

Behavioural observations were made for eight families. The families comprised of the parents, the twin older siblings, and the offspring just born. Of the eight families observed, five fell into the normal configuration described. In one family, an infant died after the first observational period, so the survivor was classified as a singleton. One family spontaneously raised triplets on two successive occasions. This situation gave one family composition of triplet offspring with twin older siblings, and another comprising triplet offspring with triplet older siblings. The data were collected during observational sessions, each of which lasted for six hours continuously. Such lengthy periods of observations are a new approach that I chose to undertake because they enabled me to collect data that would allow a better interpretation of the overall pattern of infant care. In this way I would be able to observe the sequence of events that comprise the care given to the infants, which caregivers interacted with the infant, and durations of such activities. It would also be possible to observe how the caregivers reacted to the attentions of the infants. I watched each potential caregiver for six hours at 1-2 weeks and 5-6 weeks after the birth of the infants. As the watches were spread out over a two week period, I decided to observe the caregivers in each family in a random order. The weights of the parents and juveniles were recorded, from which the mass of the carried infant as a percentage of the caregiver's body mass was calculated for each focal animal on the day it was watched.

2.6.2 Recording schedule

Data were collected during the observation sessions on an Apple II microcomputer, with 48K of random access memory (RAM) to store data whilst in

operation. The Apple 3.2 plus version disc operating system was used with autostart read only memory (ROM), printer and disc-drive interface cards (Apple Comp. Inc., Cupertino, California). The system also contained an Apple clock to add real time and date operations for intervals down to one millisecond. Additional equipment in conjunction with Apple II comprised Apple II floppy disc-drive, Maxell mini disks for use with drive, monitor and silentype micro-printer.

A programme was written in Apple II BASIC (see Appendix 3), so that each time a key was depressed on the key-board, the identity of the key and time pressed were stored in memory. This programme was an adaptation of one already used by Dr. Hubrecht. By assigning different behaviours to each key, a large number of interactions could be stored easily and accurately in the memory. Since the observation sessions were of such lengthy duration, a sub-routine 'Databack' was written into the programme to store the data on disc, so that it was not lost in the event of a power failure. At the end of the observation session the data were transferred to disc for storage. A hard copy was also made of the data in a printed form, using the micro-printer. This was done to allow visual inspection, and for initial analysis of the raw data. The data saved on disc could then be readily accessed for analysis using other analytical programmes at a later date. (See Tables 2.2 and 2.3 for a list of the keys assigned to the different behaviours).

2.7 Analysis.

The data collected were run with an analysis programme, (See Appendix 4). This programme calculated frequencies and durations of all the behaviours that had been recorded during each of the focal animal sessions. Some of the data were

totalled for each of the caregivers for a watching period, so that for some behaviours a total of 24 hours of data were collated; for example the number of grid crosses for all the caregivers might be pooled to give an indication of how active the whole family was. These totals were printed out in hard copy, and were also stored on disk for possible further use. All of the data collected for the family that raised triplets were analysed by hand, since the Analysis programme was not suitable for use in this case.

Table 2.2. Keys designated for the recording of behaviours, in the families that raised twins. C designates a control character.

Focal Animal	Infant 1	Infant 2	Behaviour
Mother	Q	U	infant climbs on
	CQ	CU	infant picked up
	A	H	infant climbs off
	CA	CH	infant rubbed off
	Z	B	infant rejected
Father	W	I	infant climbs on
	CW	CI	infant picked up
	S	J	infant climbs off
	CS	CJ	infant rubbed off
	X	N	infant rejected
Sib 1	E	O	infant climbs on
	CE	CO	infant picked up
	D	K	infant climbs off
	CD	CK	infant rubbed off
	C	M	infant rejected
Sib 2	R	P	infant climbs on
	CR	CP	infant picked up
	F	R	infant climbs off
	CF	CR	infant rubbed off
	V	.	infant rejected
<hr/>			
All focal animals :	7		horizontal grid cross
	8		vertical grid cross
	0		Databack
	!		Stop code
	-		deleted entry

For each observation session the focal animal had a series of unique presses for behaviours to be recorded. Analysis program written to deal with these codes.

Table 2.3. Keys designated for recording of behaviours in families that raised triplets. C designates a control character.

All focal animals:

Infant 1	Infant 2	Infant 3	Behaviour
O	E	U	infant climbs on
CO	CE	CU	infant picked up
K	D	H	infant climbs off
CK	CD	CH	infant rubbed off
M	C	B	infant rejected

All focal animals:

7	horizontal grid cross
8	vertical grid cross
0	Databack
	Stop code
-	deleted entry

The same keys were used for each focal animal with respect to the three infants, as there were not enough keys on the keyboard to allow individual codes to be designated. Therefore the Analysis programme used on the data collected from the families with twins could not be used for families with triplets.

CHAPTER THREE

RESULTS

3.1. Does infant carrying affect the mobility of the carrier?

The mobility of each caregiver was calculated by counting the numbers of horizontal and vertical grid crosses made per hour by the caregiver in each six hour observation period, when the caregiver was carrying respectively zero, one or two infants. These measurements are shown graphically in Fig. 3.1.1 for the families that raised twins, and Fig. 3.1.2 for the families observed with triplet infants. An examination of Figs. 3.1.1 and 3.1.2 of the rate of grids crossed, whilst carrying zero, one or two infants, shows clearly that mobility was much lower whilst carrying infants. It is also clear that the decrease in mobility was similar when carrying two infants. Upon examination of Fig. 3.1.3, it is apparent that the same trend is found when siblings are carrying infants

Figs. 3.1.1 and 3.1.2 show that the caregivers differ greatly in their activity levels. Activity levels are fairly similar for both observation periods, with families that raised triplet infants being more active than the families with twin infants. It is also evident in Fig. 3.1.3 for rates of mobility of the siblings, that the siblings with twin infants appear to be less active over the two observation periods than families with triplet infants. Siblings appear to be more active than adults in all cases, over the two observation periods, and in families with either two or three infants.

In the case of the families that raised triplet offspring, the males are clearly much more active whilst unburdened, than the females. This trend appears to be

similar for both of the observation periods. The females, whether with twins or triplets, do appear to be more mobile whilst carrying infants, although as already stated their activity levels are suppressed when carrying infants. The females often carry the infants for longer periods than the males, and therefore have to move whilst carrying infants, to feed and drink water. These habits could explain why females appear to be unhindered when carrying infants. This is especially noted in the earlier weeks of life.

As a result of this visual examination of the mobility of the caregivers, the data for the adults and siblings was further analysed. This analysis looked at the changes in mobility in the carriers when carrying infants. The statistical test used for this analysis was the χ^2 'goodness of fit' test. The results are presented in Tables 3.1.1 and 3.1.2, for adults and siblings respectively. The results combine data from families that raised both twin and triplet infants.

The general finding was that the caregivers' behaviour is greatly altered by carrying infants. In almost all cases, each individual's activity level was significantly reduced when carrying infants. Table 3.1.1 shows clearly that for the adults, most of the results were highly significantly different, with only three specimens from which data were non-significant. In one instance, female δb was ill, and so didn't move and all carrying was done by the male and siblings. Male 3 was very inactive, and carried the infants for a longer period than the female. Female 1 (from the family in which one infant died after three weeks), carried the infants more than the male, and as a consequence moved whilst carrying the infants. There were however, some exceptions, where animals appeared to be unaffected by the burden of carrying infants. For example, a female with a low overall level of activity during the day of

observation carried her infants for a substantial amount of the day, and so had to move whilst carrying the infants, thus appearing to be unhindered by carrying her offspring.

The same trend is found in the analysis of the data for the adolescent helpers, albeit not quite so significantly, in Table 3.1.2. It appears that male siblings tend to have more non-significant values for the χ^2 'goodness of fit' test, which may suggest that they are less affected by infant carrying. However the non-significant cases are generally found when the sibling has only been carrying one infant.

There is enough evidence from the data to suggest that the cases where carrying one infant did not significantly alter behaviour were exceptions, the data from them do not detract from the main conclusion that carrying infants affects the activity levels of the individual to a greater or lesser extent. The differences observed for the different caregivers, may be explained by natural variation found in these primates.

Fig. 3.1.1. Summary graphs of mean adult activity levels during both observation periods. The means and standard error of the means (S.E.M.) are shown, which are calculated from the rate of mobility per hour of caregivers from eight families, whilst carrying 0, 1 or 2 infants.

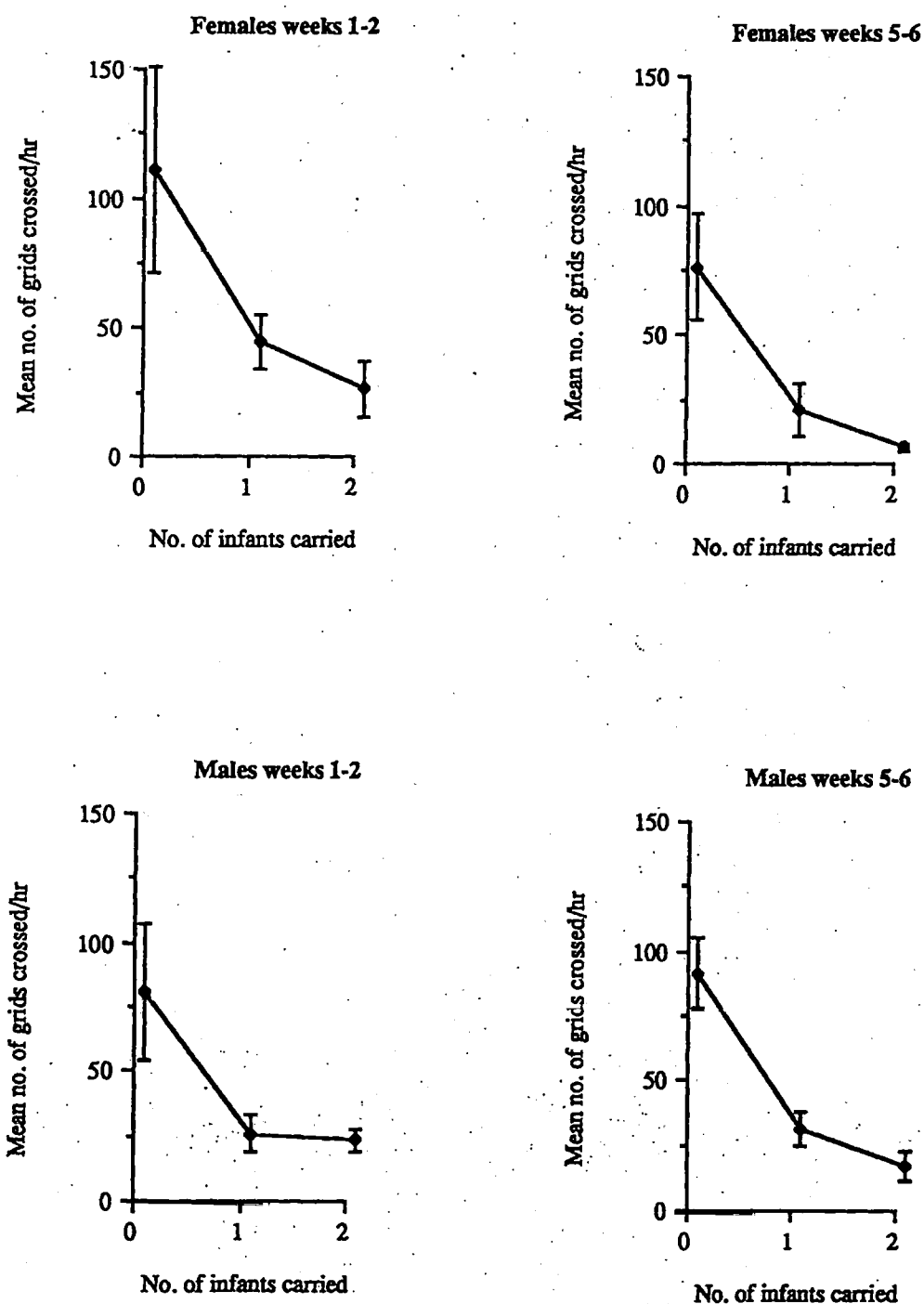


Fig. 3.1.2 Summary graphs of mean adult activity levels during both observation periods. The means and standard error of the means (S.E.M.) are shown, which are calculated from the rate of mobility per hour of caregivers from eight families, whilst carrying 0, 1, 2 or 3 infants.

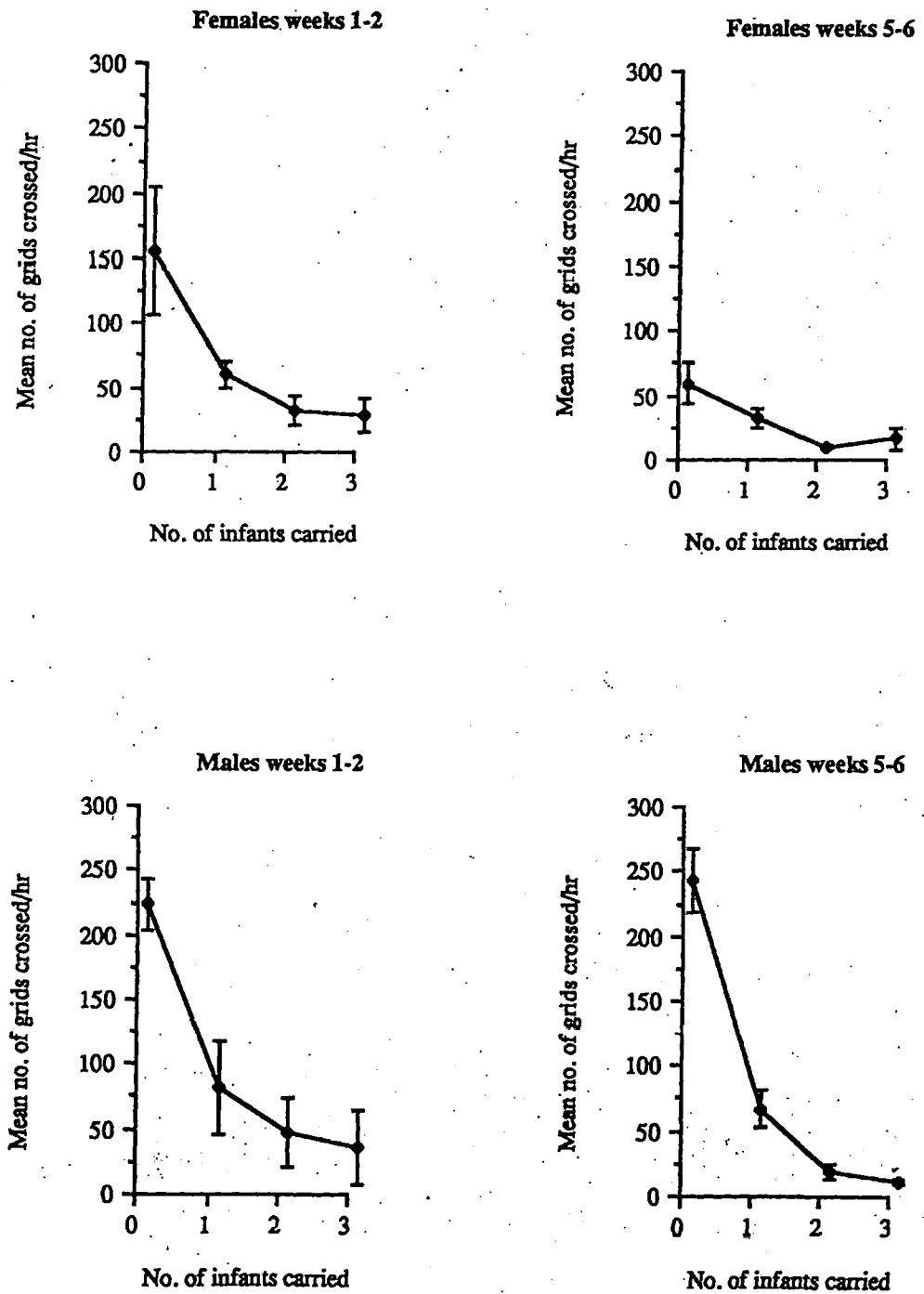


Fig. 3.1.3 Summary graphs of mean sibling activity levels during both observation periods. The means are calculated from the rate of mobility per hour of caregivers from eight families, whilst carrying infants.

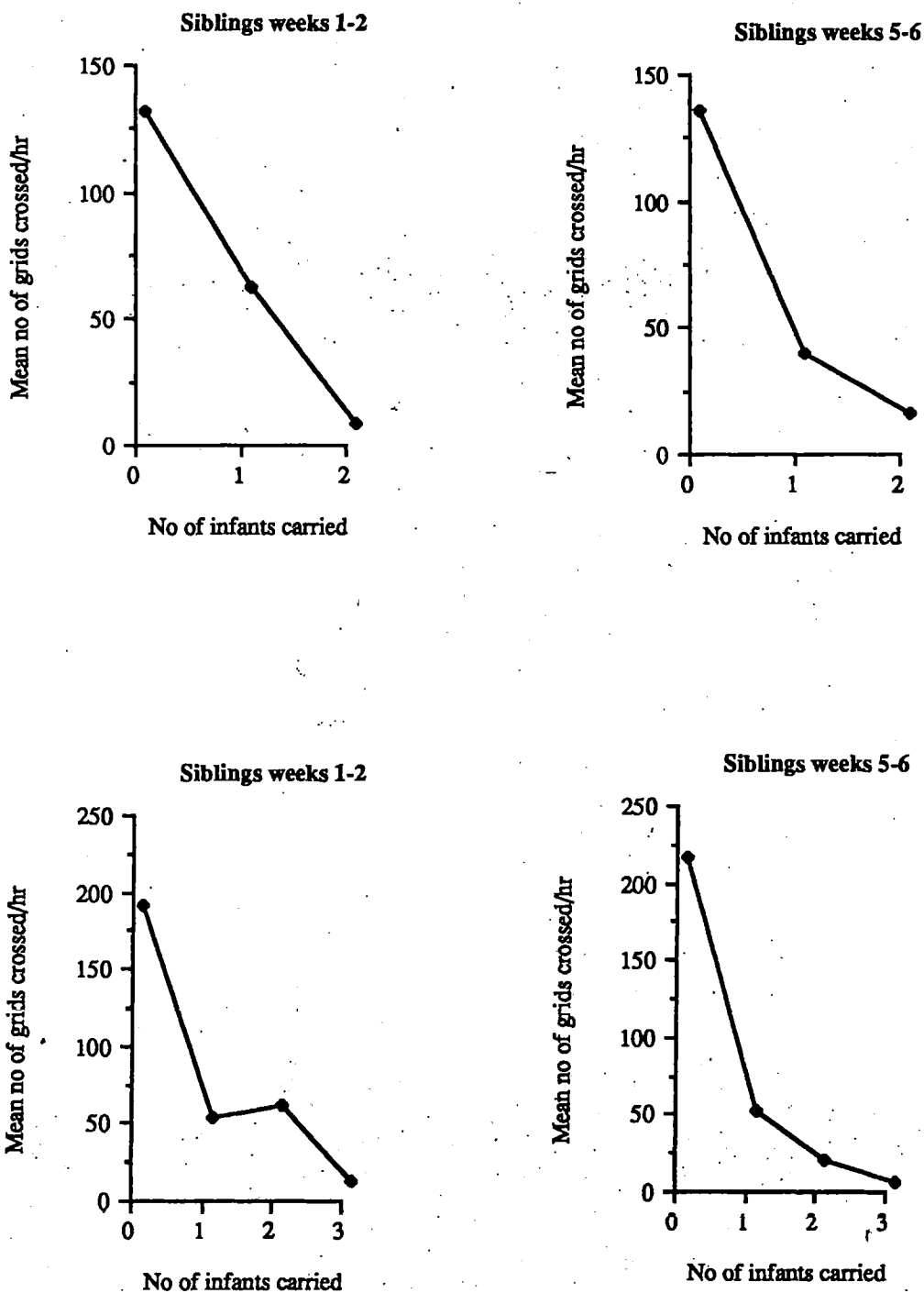


Table 3.1.1 Gives the χ^2 values for changes in mobility, of the adults, as a result of carrying infants.

Cage	Female	Male	Number of infants in the family.
<i>Weeks 1-2</i>			
1	3.2	113.3 ***	2
3	120.1 ***	5.5	2
4	156.2 ***	95.5 ***	2
8	196.0 ***	225.3 ***	2
8b	42.8 ***	157.3 ***	2
9	84.6 ***	16.7 ***	2
11a	81.4 ***	740.8 ***	3
11b	160.2 ***	33.5 ***	3
<i>Weeks 5-6</i>			
1	64.3 ***	30.7 ***	1
3	94.0 ***	36.7 ***	2
4	285.9 ***	135.2 ***	2
8	82.6 ***	254.4 ***	2
8b	0.2	201.0 ***	2
9	133.1 ***	29.2 ***	2
11a	23.4 ***	188.4 ***	3
11b	99.5 ***	871.8 ***	3

(*** significant at 0.1%)

Male 1 (weeks 1-2) and female 8b (weeks 5-6) only carried infants individually.

Cage 1 weeks 5-6 only had one infant.

Table 3.1.2 Gives the χ^2 values for changes in mobility of the siblings, as a result of carrying infants. Ic represents the maximum number of infants carried by a sibling. Ip is the number of infants available in the family to be carried.

Female sib	Ic/Ip	Male sib	Ip/Ic
<i>Weeks 1-2</i>			
2.4	1/2	84.9 ***	2/2
23.5 ***	2/2	14.5 ***	1/2
11773.0 ***	2/2	17.5 ***	2/2
45.8 ***	1/2	0.9	1/2
1.0	1/2	0.9	1/2
35.9 ***	2/2		
48.6 ***	2/3	18.9 ***	2/3
305.6 ***	2/3	255.2 ***	2/3
259.1 ***	3/3		
<i>Weeks 5-6</i>			
1.7	1/2	123.8 ***	2/2
9.2 **	2/2	109.5 ***	2/2
51.7 ***	2/2	48.2 ***	2/2
48.9 ***	2/2	4.9	1/2
8.0 *	1/1	5.6 *	1/1
728.0 ***	2/2	0.6	2/2
12.0 **	3/3	1.2	1/3
172.1 ***	2/3	22.3 ***	2/3
15.4 **	2/3		

(* sig. at 5%: ** sig. at 1%: *** sig. at 0.1%)

Ic/Ip: Denotes the ratio of the maximum number of infants carried by the caregiver to the total number of infants in the family.

3.2. Are infants more likely to be carried simultaneously or sequentially?

Having established that there is a reduction in mobility whilst carrying infants, I predicted that the caregivers would minimise impairment of mobility by carrying infants together rather than individually. Since impairment of mobility is approximately equivalent when carrying either one or two infants, carrying two infants would minimise the time spent by the caregiver in the burdened state. To investigate this hypothesis I undertook an analysis of the data using the *Log Likelihood Ratio* test (Basana & Rao 1980), which is described in Appendix 2.1. (The test I used was an adaptation of the above mentioned test, and the adaptation was carried out by Dr. K. McConway.) The test compares the three states in which a caregiver may be found.

State 0, when the caregiver is not carrying any infants.

State 1, when the caregiver is carrying one infant.

State 2, when the caregiver is carrying both infants.

An assumption was made that the caregiver only steps from one state to the next, and cannot jump two states. For example, a caregiver does not go from carrying zero to two infants without carrying one for a short period. The *Log Likelihood Ratio* tests the null hypothesis that the 3-state process is the sum of two independent 2-state random processes. In other words, the decision to carry one infant is not dependent upon whether or not the other infant is being carried. In this analysis, carrying each infant is a state. Under the null hypothesis, the caregiver treats each of the two offspring independently, picking up or putting down each one regardless of whether or not the other is already being carried. The results of this test are shown in Table 3.2.1 for the adults and Table 3.2.2 for the siblings.

Table 3.2.1 Test statistics for the Log Likelihood Ratio test: Adults

CAGE	Weeks 1-2		Weeks 5-6	
	Female	Male	Female	Male
1	6.3 *	3.5	-	-
3	6.6 *	4.2	64.9 ***	37.2 ***
4	4.2	8.7 *	39.9 ***	58.3 ***
8	15.1 ***	3.8	51.5 ***	34.9 ***
8b	14.4 ***	2.6	-	27.5 ***
9	<u>41.0</u> ***	<u>4.6</u>	<u>90.3</u> ***	<u>48.5</u> ***
Total	67.7 ***	27.3 ***	246.7 ***	206.5 ***

* sig. at 5%: **sig. at 1%: *** sig. at 0.1%

All the values for the males and females in weeks 5-6 are significant to 0.1%.

All the summed values were significant at 0.1%

Cage 1 had only one infant during the second observation period.

Cage 8b, the female only carried one infant during observation, because she was ill.

Table 3.2.2 Test statistics for the Log Likelihood Ratio test: Siblings

Weeks 1-2		Weeks 5-6	
Sib1 (f)	Sib2 (m)	Sib1 (f)	Sib2 (m)
33.2 ***	17.1 ***	35.9 ***	12.4 **
<u>7.6</u> *	9.1 *	142.5 ***	9.9 **
	<u>92.9</u> ***	39.4 ***	38.7 ***
		<u>14.9</u> ***	<u>44.1</u> ***
Total 40.6 ***	119.1 ***	232.8 ***	105.1 ***

* sig. at 5%: **sig. at 1%: *** sig. at 0.1%

All the summed values for the male and female are significant to 0.1%.

m = male: f = female.

The summed values of the Log Likelihood Test clearly show that the infants are not picked up independently, and that the caregivers show a tendency to be in state 2 rather than state 1, as shown in Tables 3.2.1 and 3.2.2.

For the later observation period, the results for the adults and siblings show

that there is a greater probability of finding the caregiver in state 2 than state 1. The same is the case for the siblings at the earlier observation period. When comparing the adults for weeks 1-2, it is possible to say that there is an overall trend (by summing the values), to be in state 2. However the results for the males in weeks 1-2 show that they are more often in state 1, suggesting there may be a tendency to carry uncared for infants in order that they are constantly carried.

By examining the tables more closely, it is obvious that not all adults in the earlier test period follow this trend. Among the females, there is only one exception, which carried the infants for most of the day, and as a consequence was mobile even while carrying both infants. However her overall rate of activity was much lower than that of the other females. The data from individual males suggests a tendency to carry two infants rather than one, but due to the relatively small number of observations for each individual it was not possible to get more conclusive data. As seen in Table 3.2.1 the values from individual adult males were not all significantly different, but when summed together follow the trend, whereas in all other cases the individual values are significant.

3.3 Rate of infant transfer in the different carrying states.

Having established that infants tend to be carried together significantly more often as pairs than individually, I investigated the rates of pick-ups and climb-ons in each of states 0 and 1. State 0 is the state when the caregiver is not carrying any infants; states 1 and 2 denote when the caregiver is found to be carrying one or two infants respectively. (The test used is described in Appendix 2) The results are listed in Table 3.3.1 for the adults and 3.3.2 for the siblings. The rates of climb-offs and rub-offs were also analysed in the same manner, (Appendix 2), and the results shown in Table 3.3.3 for the adults and 3.3.4 for the siblings. I examined the migration rate of the infants whilst the caregivers were in each of states 0, 1 or 2, to establish whether there were differences in rates of infant migration when caregivers were in state 0, 1 or 2. I predicted that the rate of migration would be greatest in state 1, since I had established a preference for carrying infants simultaneously rather than individually. *Migration* of an infant is described as the transfer of an infant from one caregiver to another. The infant may be passively transferred by the caregivers, or may voluntarily move onto and off the caregivers.

The results in Tables 3.3.1 and 3.3.3 reveal that, although in weeks 1-2, the results for rub-offs and climb-offs are not individually significant for the males and females, there may be a trend showing an increased rate of migration when the caregiver is carrying only one infant. When the individual Z values are squared and summed there is a group significance. In the case of the males, weeks 1-2 pick-ups and climb-ons, the pooled group data are significantly different. In the case of the female weeks 1-2 the pooled Z statistics are not quite significant, but do suggest that there was an increased rate of movement of

infants when in state 1.

The results in Tables 3.3.1 and 3.3.3, show that in the later observation period there is a difference in the rate of infant movement, and that this is greater when the caregiver is in state 1. The data suggest that either the infant or the caregiver, or both, prefer to be in either state 2 or state 0; that is, carrying the infants together or having no infant load at all. This general finding for individuals was highly significant when the individual results were pooled together.

The results for the siblings in Tables 3.3.2 and 3.3.4, show that the rub-off and climb-off rates were insignificant at weeks 1-2 and highly significant at weeks 5-6 with more movement when in state 1. They may prefer to be in state 0, but the siblings respond to the distress calls of infants that are not being carried. They pick up the infant and may instantly try to rub it off, giving rise to many very brief periods of carrying, and rarely try to carry two infants. Older siblings are larger and thus more able to carry the infants for longer periods.

It is not possible to assess whether it is the infants or the adults that are responsible for the observed tendency for the infants to be carried in pairs, as the data sets are too small for any full investigation. However, by looking at the rates of exchange between carriers it is possible to give values for the spontaneous changes made by the infants, that is, where the infants climbed onto, or off the caregiver, rather than being picked up or rubbed off. The analysis used followed Kohda (1985); Table 3.3.5 shows rates of spontaneous changes $\times 100/\text{total number of infant transfers}$. As can be seen in Table 3.3.5, in most instances the infants initiate being carried in pairs. In the early

observation session, the data from the males suggest the opposite is the case, with the males actively picking up the infants, both the first and the second infants in the pair bouts.

Table 3.3.1. The pick-up and climb-on rates for mother and father for the two age periods, also showing the S.E. and Z statistic. The Z value is squared, then totalled to produce the χ^2 value shown.

CAGE	λ_0	λ_1	S.E.	Z	z^2	λ_0	λ_1	S.E.	Z	z^2
Mother weeks 1-2						Father weeks 1-2				
1	0.0	1.7	3.4	0.5	0.2	0.7	0.0	0.4	2.0*	4.0
3	1.2	3.2	1.6	1.2	1.4	1.8	3.2	1.5	1.0	1.0
4	6.4	6.4	4.5	0.0	4×10^{-6}	1.9	4.4	2.6	9.9***	99.7
8	0.9	6.4	2.7	2.1*	4.2	2.6	2.3	1.4	0.2	0.0
8b	0.8	6.6	2.7	2.1*	4.6	1.9	2.7	1.4	0.6	0.3
9	0.7	44.6	19.9	2.2*	<u>4.8</u>	1.8	3.5	2.0	0.3	<u>0.1</u>
Total χ^2					15.3	105.2***				
Mother weeks 5-6						Father weeks 5-6				
1	-	-	-	-	-	-	-	-	-	-
3	2.4	25.8	9.8	2.4*	5.8	3.2	19.2	3.9	4.0***	16.2
4	2.5	13.5	4.6	2.4*	5.8	2.6	21.3	6.7	2.8**	7.6
8	3.2	19.7	5.1	3.1**	9.8	4.5	16.3	3.7	3.2**	9.9
8b	-	-	-	-	-	8.2	16.3	3.3	2.4*	5.9
9	3.1	13.1	5.9	1.7	<u>2.9</u>	3.9	21.0	5.9	2.9**	<u>8.2</u>
Total χ^2					24.3**	48.0***				

λ_0 Estimated pick-up/climb-on rate per infant, in state 0 (pick-ups per hour) see Appendix 2.2

λ_1 Estimated pick-up/climb-on rate per infant, in state 1 (pick-ups per hour)

* sig. at 5%; ** sig. at 1%; *** sig. at 0.1%

Table 3.3.2 The pick-up and climb-on rates for siblings for the two age periods, also showing the S.E. and Z statistic. The Z value is squared, then totalled to produce the χ^2 value shown.

λ_0	λ_1	S.E.	Z	z^2	λ_0	λ_1	S.E.	Z	z^2
Female sib weeks 1-2					Male sib weeks 1-2				
24.7	0.6	8.7	2.8	7.6	0.8	0.9	0.9	0.1	0.0
0.3	1.2	1.1	0.8	0.6	0.9	1.5	1.6	0.4	<u>0.2</u>
0.5	7.8	5.5	1.315	<u>1.7</u>					
Total χ^2				9.9*					0.2
Female sib weeks 5-6					Male sib weeks 5-6				
3.1	18.6	6.6	2.3*	5.5	3.8	12.7	3.4	2.7*	7.1
0.04	0.2	0.1	1.0	1.0	2.1	6.2	3.6	1.1	1.3
2.2	22.8	8.6	2.4*	5.7	118.6	10.9	46.1	2.3	5.4
4.3	13.7	4.9	1.9	<u>3.7</u>	0.8	7.5	7.5	0.9	<u>0.8</u>
Total χ^2				15.9*					14.6

λ_0 Estimated pick-up/climb-on rate per infant, in state 0 (pick-ups per hour)

λ_1 Estimated pick-up/climb-on rate per infant, in state 1 (pick-ups per hour)

* sig. at 5%: ** sig. at 1%: *** sig. at 0.1%

Table 3.3.3. The rub-off and climb-off rates for mother and father for the two age periods, also showing the S.E. and Z statistic. The Z value is squared, then totalled to produce the χ^2 value shown.

CAGE	μ_1	μ_2	S.E.	Z	Z ²	μ_1	μ_2	S.E.	Z	Z ²
Females weeks 1-2						Males weeks 1-2				
1	0	1.2	0.5	2.4*	5.9	1.3	0.0	0.6	2.0*	1.0
3	7.2	2.1	2.6	1.9	1.9	4.3	1.7	1.7	1.6	2.4
4	3.1	0.6	1.9	1.4	1.9	28.0	6.8	7.5	2.8**	7.9
8	6.4	1.5	2.7	1.8	3.3	3.2	1.0	1.3	1.7	2.8
8b	6.6	2.4	2.8	1.5	2.1	10.0	4.6	3.4	1.6	2.45
9	71.3	9.7	25.6	2.4*	<u>5.8</u>	2.6	0.5	1.5	1.4	<u>1.9</u>
Total χ^2					22.7*					21.5*
Females weeks 5-6						Males weeks 5-6				
1	-	-	-	-	-	-	-	-	-	-
3	88.3	6.4	18.2	4.5***	20.2	15.1	7.8	3.8	1.9	3.6
4	18.1	1.5	5.2	3.2**	9.98	48.9	5.5	10.4	4.2***	17.6
8	34.2	6.6	6.9	3.9***	15.9	21.9	6.4	4.4	3.5***	12.2
8b	-	-	-	-	-	24.9	8.6	4.1	3.9***	15.7
9	68.1	1.8	13.4	4.9***	<u>24.6</u>	21.0	1.8	3.3	5.9***	<u>34.3</u>
Total χ^2					70.6***					83.4***

μ_1 estimated put down/climb-off rate per infant, in state 1 (climb-offs per hour) see Appendix 2.3

μ_2 estimated put down/climb-off rate per infant, in state 2 (climb-offs per hour)

* sig. at 5%: ** sig. at 1%: *** sig. at 0.1%.

Table 3.3.4. The rub-off and climb-off rates for siblings for the two age periods, also showing the S.E. and Z statistic. The Z value is squared, then totalled to produce the χ^2 value shown.

CAGE	μ_1	μ_2	S.E.	Z	Z^2	μ_1	μ_2	S.E.	Z	Z^2
Female sib weeks 1-2						Male sib weeks 1-2				
	0.0	0.9	0.9	0.9	0.8		5.9	3.4	4.1	0.6
	2.3	20.0	20.1	0.9	0.8		13.8	375.0	375.0	0.9
	2.2	1.1	1.2	1.0	<u>1.1</u>					
Total χ^2					2.7					1.3
Female sib weeks 5-6						Male sib weeks 5-6				
	79.2	21.9	15.4	3.7	13.8**		25.5	8.9	5.2	10.1**
	141.5	115.4	85.6	0.3	0.0		62.3	3.9	11.6	25.3***
	261.8	1.2	53.5	4.9	23.8***		237.3	500.0	507.9	0.5
	34.3	1.4	7.7	4.2	<u>17.9***</u>		67.5	100.0	102.5	3.2
Total χ^2					55.4***					45.7***

μ_1 estimated put down/climb-off rate per infant, in state 1 (climb-offs per hour)

μ_2 estimated put down/climb-off rate per infant, in state 2 (climb-offs per hour)

* sig. at 5%: ** sig. at 1%: *** sig. at 0.1%.

Table 3.3.5 The rates of spontaneous infant transfers, when the first infant is carried in a pair carrying bout, and the way in which the second infant comes to be carried. The rates of transfer are also given for the first and second infant to leave the caregiver in a pair-carrying bout.

Rate of Spontaneous transfers	WEEKS 1-2		WEEKS 5-6	
	Mother	Father	Mother	Father
First infant on	53.6%	37.0%	89.7%	82.1%
second infant on	61.4%	29.6%	90.2%	85.6%
First infant off	87.2%	95.5%	91.4%	92.9%
second infant off	65.0%	84.2%	72.7%	75.7%

$$\text{Rate of spontaneous transfers} = \frac{\text{spontaneous changes}}{\text{total no. of infant transfers}} \times 100$$

Kohda (1975).

3.4 Differences in mean carrying bout length, and mean numbers of carrying bouts, in the different infant-carrying states.

The duration of carrying bouts and mean number of carrying bouts performed by the caregivers in each of the carrying states were measured. The mean bout lengths were analysed for differences between the adults and between the observation periods. Results obtained for the male and female siblings were also compared with each other and with the adults, for each observation period and between the two age periods studied. The carrying bouts were divided into single infant carrying bouts and those when two infants were carried.

Comparisons were also made between the caregivers and the mean number of carrying bouts performed in each of the carrying states. Comparisons were also made between the families that raised twins and those with triplets.

Number of carrying bouts.

State 1 - carrying one infant.

Adults - During both weeks 1-2 and 5-6 there are no differences between the number of carrying bouts per session for male and female adults. This applies to the parents of both twin and triplet families. For families with twin infants, between 1-2 weeks and 5-6 weeks old, in Table 3.4.1a, for combined data from adults, there is a difference in the number of carrying bouts, with more bouts occurring in weeks 5-6.

Siblings - No differences were found between male and female siblings at the two different age periods. When comparing the two periods; a difference was found between families with twins in weeks 1-2 compared with weeks 5-6; and families with triplets in 1-2 weeks were compared with families in 5-6 weeks in

Table 3.4.1b, again with more carrying bouts being performed in the later observation period.

Adults compared with siblings - Examining the data between the adults and siblings showed that there were no differences between them. There were also no differences found when comparing families with twins or triplets in the later age period. However the adults executed more carrying bouts than the siblings did in the case of the twin families in the earlier observation period, although this difference was not observed in the case of the families with triplet infants.

State 2 - carrying two infants.

Adults - There were no differences between number of carrying bouts performed by the mother and father when carrying both infants in weeks 1-2. However, in weeks 5-6 in Table 3.4.2a, males exhibited a higher carrying frequency than females. This difference is not significant for families that raised triplets where the number of carrying bouts between the adult males and females were similar in weeks 1-2 and 5-6.

Data from males and females were combined for weeks 1-2 as they were not different, and compared with data from males and females separately, collected in weeks 5-6, as seen in Table 3.4.2a, and it was found that more carrying bouts were performed in the later period of infant care.

Table 3.4.2b shows that in families that raised triplets, the number of carrying bouts with two infants differed between the two observation periods. When examining families with twins and triplets, there is a difference in the number

of pair carrying bouts in weeks 5-6 between those families with twin infants and those with triplet infants.

Siblings - There were no significant differences in the data from the siblings, so I combined the data for the sexes and looked for differences between the observation periods. All differences found are listed in Table 3.4.2b. The triplet families were not compared, as there were insufficient data.

State 1 compared with state 2

Number of carrying bouts - The time spent by each caregiver carrying either one infant or carrying a pair of infants was compared. Both adult males and females differed between states one and two with respect to the number of carrying bouts made in states one and two. Two findings were made, firstly that more carrying bouts occurred during the later observation period than in the first weeks of life; and secondly that more carrying bouts were performed in state one, again indicating that there is most infant migration occurring in state 1. Male siblings were found to perform a greater number of carrying bouts in the later observation period than female siblings.

When the data from each of the caregivers were combined and then examined for differences between the observation periods, whilst carrying one infant or both infants, differences were found. There were more carrying bouts in the later observation period.

Single infants $t = -5.355$ $p < 0.001$

Pairs of infants $t = -3.718$ $p < 0.005$

Table 3.4.1a The mean number of carrying bouts performed by the adult caregivers whilst carrying one infant. (N=6)

weeks 1-2		weeks 5-6	
mother(1)	father(2)	mother(3)	father(4)
13	13	32	41
9	22	21	34
12	12	41	49
13	7	31	25
6	5	18	14
12	19	1	71

Adults of families with triplets

(5)	(6)	(7)	(8)
7	11	75	52
8	14	29	42

Table 3.4.1b The mean number of carrying bouts performed by the sibling caregivers whilst carrying one infant. (N=6)

female(9)	male(10)	female(11)	male(12)
9	8	11	45
2	4	20	24
0	10	42	10
3	5	32	8
3	2	20	31
9	1	29	8

Siblings of families with triplets (N=2)

(13)	(14)	(15)	(16)
6	4	14	8
8	9	26	29
8	-	18	-

Statistical assessment of differences between columns, numbered (1) to (16).

T-test comparisons made between all columns.

1+2 and 3+4 $t = 3.61$ $p < 0.05$

1+2 and 9+10 $t = 4.15$ $p < 0.001$

9 and 11 $t = 4.81$ $p < 0.001$

5 and 7 $t = 4.01$ $p < 0.05$

13 and 15 $t = 3.04$ $p < 0.05$

All other comparisons were not significantly different.

Table 3.4.2a The mean number of carrying bouts performed by the adult caregivers whilst carrying pairs of infants. (N=6)

weeks 1-2		weeks 5-6	
mother(1)	father(2)	mother(3)	father(4)
4	6	7	3
7	3	9	10
6	4	15	21
6	-	-	-
5	5	5	14
6	4	-	29

Adults of families with triplets (N=2)

(5)	(6)	(7)	(8)
12	9	48	20
9	4	19	7
5	3	15	28
1	0	6	14

Table 3.4.2b The mean number of carrying bouts performed by the sibling caregivers whilst carrying pairs of infants. (N=6)

female(9)	male(10)	female(11)	male(12)
1	1	15	9
-	1	-	2
-	-	4	7
1	-	1	-
-	2	-	9

Siblings of families with triplets (N=2)

(13)	(14)	(15)	(16)
1	1	3	-
-	-	1	-
1	2	-	3
2	-	2	-
1	-	1	-

Statistical assessment of differences between columns, numbered (1) to (16).

T-test comparisons made between all columns.

3 and 4 $t = 2.45$ $p < 0.05$

2 and 4 $t = 4.42$ $p < 0.05$

9+10 and 11+12 $t = 2.72$ $p < 0.05$

1+2 and 3 $t = 2.87$ $p < 0.01$

1+2 and 4 $t = 6.41$ $p < 0.001$

5+6 and 7+8 $t = 2.50$ $p < 0.05$

3+4 and 11+12 $t = 2.48$ $p < 0.05$

All other comparisons were not significantly different.

Mean bout lengths.

State 1 - carrying one infant

Adults - The mean bout lengths of adults were compared in the two observation periods. The mean bout lengths were also compared for adults raising twins or triplets. Differences were found, indicating that mean bout lengths were not similar for all caregivers and for both time periods for which data were collected. The only difference found in mean bout length was between females with triplets in weeks 1-2 and triplet female weeks 5-6 in Table 3.4.3a, with the females with triplets carrying for significantly longer in the first two weeks of life.

Siblings - The data from male and female siblings in the two observation periods were compared in Table 3.4.4b, the only significant difference found was between males and females of twin families in weeks 1-2, where the mean bout length was greater for the females.

When comparing male and female siblings with twin or triplet infants no differences were found within observation periods or within sex groups.

When comparing female and male siblings between the two observation periods the following differences were observed in Table 3.4.4b. Female and male siblings in families that raise twins performed longer carrying bouts in the earlier period of infant care than when infants were older. This is also true of female siblings in families with triplet infants.

By combining the data for male and female siblings of families rearing triplets, an observation-period difference was found, although the difference observed for males between weeks 1-2 and 5-6 is not significant.

Adults compared with siblings - Comparison of adults and siblings over

the two observation periods produced no significant differences. No sex differences were found in mean carrying bout length. The only difference observed was between adults and siblings at weeks 5-6 when comparing values in Tables 3.4.4a and 3.4.4b.

State 2 carrying both infants.

Adults - Differences were found between the mean lengths of the pair-carrying bouts for males and females for both observation periods. This was also true for adults with triplet offspring. When all the data from the adults were combined there was a difference between the observation periods, in Table 3.4.4a.

Siblings - No differences found in the mean lengths of carrying bouts for siblings, between the two data collection periods, or between the sexes or between siblings in families raising triplets, carrying two or three infants.

State 1 compared with state 2.

Mean bout lengths were also compared for each of the caregivers between the two states, and few differences were found. In weeks 1-2, the mean bout lengths for male siblings in state one differed from male siblings in state 2, and in weeks 5-6,. Mean durations were found to be greater in the earlier observation period.

When combining data for all caregivers, differences were found in both state one and two, between the two observation periods. The mean duration of carrying bouts was greater during the first two weeks of life.

Single infant $t = 3.115$ $p < 0.005$

Pairs of infants $t = 3.871$ $p < 0.001$

Table 3.4.3a The mean duration of carrying bouts (seconds) performed by the adult caregivers whilst carrying one infant. (N=6)

weeks 1-2		weeks 5-6	
mother(1)	father(2)	mother(3)	father(4)
347	512	30	110
374	115	113	49
279	654	52	92
31	595	44	89
2066	2207	605	88
274	283	-	387

Adults of families with triplets (N=2)

(5)	(6)	(7)	(8)
1164	591	38	36
745	356	114	50

Table 3.4.3b The mean duration of carrying bouts (seconds) performed by the sibling caregivers whilst carrying one infant. (N=6)

female(9)	male(10)	female(11)	male(12)
700	528	36	94
668	106	21	72
1040	235	23	48
620	123	48	29
48	182	26	20
1256	-	72	13

Siblings of families with triplets (N=2)

(13)	(14)	(15)	(16)
407	124	16	19
965	1060	104	24
962	-	14	-

Statistical assessment of differences between columns, numbered (1) to (16).

T-test comparisons made between all columns.

Adults

5 and 7	t = 4.13	p < 0.05
1 + 2 and 3+4	t = 2.21	p < 0.05
9+10 and 11+12	t = 3.95	p = 0.001

Siblings

9 and 10	t = 2.45	p < 0.05
9 and 11	t = 4.05	p < 0.05
10 and 12	t = 2.67	p < 0.05
13 and 15	t = 3.93	p < 0.05
13+14 and 15+16	t = 3.52	p < 0.01

Adults wks 5-6 and siblings wks 5-6 t = 2.09 p < 0.05.
All other comparisons were not significantly different.

Table 3.4.4a The mean duration of carrying bouts (seconds) performed by the adult caregivers whilst carrying pairs of infants. (N=6)

weeks 1-2		weeks 5-6	
mother(1)	father(2)	mother(3)	father(4)
834	1055	267	211
2475	243	1152	262
1178	1417	214	229
747	394	-	203
1482	-	-	-

Adults of families with triplets (carrying two infants) (N=2)

812	361	42	36
1932	88	172	145

Adults of families with triplets (carrying three infants) (N=2)

319	851	130	284
1761	-	222	668

Table 3.4.4b The mean duration of carrying bouts (seconds) performed by the sibling caregivers whilst carrying pairs of infants. (N=6)

female	male	female	male
523	2101	208	82
-	87	-	13
-	-	415	47
4	-	20	-
-	1708	-	1139

Siblings of families with triplets (pairs) (N=2)

156	50	17	-
34	57	-	36
370	-	19	-

siblings of families with triplets (triplets) (N=2)

857	-	13	-
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Statistical assessment of differences between columns, numbered (1) to (16).

T-test comparisons made between all columns.

Adults

1+2 and 3+4 $t = 2.15$ $p < 0.05$

All other comparisons were not significantly different.

3.5 PRINCIPAL RESULTS FROM THE STUDY.

1. There is a significant reduction in movement of the caregivers observed whilst they are carrying infants, but mobility is as much affected by one as by two infants, and is equally evident shortly after birth and when the infants are older. These findings apply to both the adults and older siblings.
2. Infants appear to be carried together as a pair by the caregiver, rather than singly.
3. Rate of infant climb-ons and climb-offs tend to be greater when a caregiver has one infant, than when carrying zero or two infants. From the data collected, it is not possible to determine whether the infant transfers are initiated by the infant or by the adult.
4. The number of carrying bouts differs between the two observation periods, with more carrying bouts occurring in the later period of infant care. When all data for the caregivers is combined, and the observation periods are examined for differences, it is apparent that the average bout duration is greater in the first two weeks of life. That is there are fewer longer carrying bouts during the first weeks of life.

3.6 CONCLUSION

The data show that carrying one infant affects mobility, and that there is a tendency for infants to be carried together rather than individually. It is interesting that the rate of migration of the infants is such that it acts to minimise the amount of time that a carer spends carrying just one infant. Migration comprises two different processes, one is the infant's active role of climbing onto or off the caregiver; the second is the passive role of the infant, when a caregiver actively picks up or rubs off the infants. Since there were not enough data to make a distinction between the active and passive roles of the infant, I have analysed the data ignoring this distinction. It would appear, however, that by looking at the rates of spontaneous infant transfer, that the infants may be determining the duration and state of the carrying bouts. A caregiver could minimize time spent with reduced mobility by carrying both infants at once.

CHAPTER FOUR

DISCUSSION

4.1 INTERPRETATION OF THE RESULTS FROM THE STUDY.

The principal aim of the study was to determine how marmoset monkeys (*Callithrix jacchus*) adapt their behaviour to the demands of carrying twin infants. As previously discussed, the female produces twin offspring, and may almost immediately become pregnant again, thus being burdened by having to carry and suckle the infants, with the next litter *in utero*. These factors may impose great energetic demands upon the female. It has been postulated that the system of infant care which involves all members of the family carrying the infants that has evolved in the Callitrichidae, reduces the burden on the mother.

The results of the present study show clearly that the act of carrying infants effects the activity of the caregivers. It is not possible to show whether the caregivers' activity is reduced as a result of carrying the infants, or if the infants are carried whilst the caregivers are inactive. I would postulate that it is likely to be a combination of factors. Thorough analysis of the data from both the perspective of loss of mobility whilst carrying and how the carrying bouts are structured, indicate the means by which the family copes with the demands of caring for the newly-born infants.

One of the major findings of the study reveals that the activity of the caregiver carrying the infants is severely reduced, as shown in Figs. 3.1.1, 3.1.2, and 3.1.3. Carrying a single infant reduces mobility as much as carrying two, or three, infants. It would thus appear that if mobility is reduced in this way then

the caregiver can minimise the time spent in the state of carrying infants by being burdened by two infants for a shorter period of time, rather than by carrying the infants individually for longer. These conclusions are borne out by the analysis of the data shown in Tables 3.1.1 and 3.1.2. They show that mobility is significantly decreased as a result of carrying infants. Soule *et al.* (1987) found that in humans energy expenditure increased when carrying loads at high speed; although energy expenditure did not rise as the loads were increased if speed remained low. Thus if increases in speed are generally associated with a greater increase in energy expenditure than an increase in load, it may be that the marmoset caregiver may raise its energy output whilst carrying one infant, with only a small rise in energy output whilst carrying the second infant. It should be noted that marmoset locomotion is mostly climbing and jumping, and their conclusions are only established for walking and so the comparison may not be apt. Nonetheless the caregiver could reduce the time spent with reduced mobility by carrying both infants at the same time.

Whilst studying marmosets at the field site of Tapacura, Brazil, Scanlon (pers. comm.) observed that families with infants appeared to be less active within their territories, than groups that did not contain infants. These observations agree with the measurements on captive marmosets made in the present study.

The second major finding from the study is that the infants are more often carried together as a pair by the caregiver. During the first three weeks of life the infants are carried continuously by one of the family members (Anzenberger pers. comm.; pers. obs.). He suggests that in the early stages of their post-natal care the father actively ensures that the infants are carried. The results from the *Log Likelihood Ratio* test support the idea that the infants are carried together, and that there is a tendency for the caregiver not to remain in the state

of carrying only one infant, as shown in Table 3.2.1 for the adult carriers and in Table 3.2.2 for the siblings. This tendency is not apparent in the case of the males in the earlier observation period, and may be indicative of some sort of compensatory behaviour that ensures that the infants are cared for continuously in the vulnerable stages of life. The adult male, being the primary caregiver, has to initiate actively the carrying of the infants. He carries the infants when other caregivers no longer respond to the infants. There is a high demand for infant care, especially in the first two weeks. Box (1975b) found that the caregivers may carry one infant in preference to carrying two. Although similar overall trends were seen in this study, there was great variability within individual families encompassing several different caring regimes that provide proper care and protection for the infants. Box's results may differ from those found in the present study, because her study families were generally larger than those used here.

The third finding from the results is that there appears to be a great deal of infant transfers taking place when the caregiver is in the state of carrying one infant. It is not obvious whether such behaviour is initiated on the part of the adult or infant, or indeed whether there is a tendency to avoid carrying any infants. The χ^2 values in Tables 3.3.1, 3.3.2, 3.3.3, and 3.3.4, show that there is a group significance, although the data are not significant for all individuals. The trend is stronger in the case of the adults than the siblings.

Table 3.3.5 shows that the infants may be climbing onto the mother and father in both age periods to a greater extent than being picked up by them. However the males did not behave similarly in the earlier observation period. Here it would seem that the males are actively picking up the infants, consistent with the idea that the males are ensuring that the infants are always carried. Box(1975b) did

not find this to be the case. Examination of the rate of spontaneous infant transfer, (climb-ons and climb-offs), show that the rate of climb-offs is greater when the caregiver is in state two, and exceeds the rate of climb-ons that occur to bring the carer into the state two, showing that the infants maybe determining the length of the carrying bouts. Once one infant has decided to leave the caregiver, the remaining infant also leaves spontaneously more often than being forcibly rubbed off. This difference is very clear for both parents during the later observation period.

The fourth finding of the study is that the average carrying bout length for both adults and siblings at both of the observation periods appears to be greater during the first weeks of life. The mean number of carrying bouts performed by all the caregivers appears to be greater in the later period of infant care, as seen in Tables 3.4.3a, 3.4.3b and Tables 3.4.4a, 3.4.4b. Thus it appears that there are fewer longer carrying bouts in the first weeks of life.

It is perhaps not surprising that the mean bout lengths should be greater during the earlier period of infant care, since it is during the first weeks of life that the infants need constant care and attention. The siblings perform slightly longer carrying bouts in state one, in the earlier weeks of life. This mechanism may ensure that the infants are continually cared for. Pryce (1988) has postulated that there is some form of regulation within the family that ensures that the infants are constantly cared for. McGrew (1988) observed that the greater the number of adolescent helpers there are in the family, the less carrying the father does.

The numbers of carrying bouts performed by the caregivers are greater during the later period of care, than in the first weeks of life. In weeks 5-6 there were

more carrying bouts in state one, which accords well with the findings that there is the greatest degree of infant migration taking place in state 1. It is therefore not yet possible to assess how the amount of care the infant receives is regulated.

Locke-Haydon & Chalmers (1983) suggest that there is no compensatory behaviour that ensures the infants are properly cared for in the first few important weeks of life. In fact, they suggest that if there is one caregiver with a low rate of carrying, the whole family may be the same. This conclusion is in conflict with data from Anzenberger (pers. comm.) and Arruda *et al.* (1986), who showed that for the first 3 weeks the infants are always carried, even though by different caregivers. Observations made during this study tend to support the latter conclusion that there may be some form of compensatory caregiving behaviour taking place.

The female initiates the feeding bouts, this may be because she can not 'feed on demand'. Pryce (1988) has postulated that the male may in some way regulate the amount of carrying done by the female. My observations support this, as I have observed a family that spontaneously raised two successive sets of triplets. It appeared that the infant 'neglected' on one day was carried to a greater extent by the female the next day, possibly to compensate for less feeding on the previous day. If the ability of families to equalise for the caring that they give to their infants is variable, then not all families would be able to raise triplets. In the wild situation, triplet infants have not been reported to date. It may also be that the increased incidence of triplet infant births in captivity, may arise from the improved nutritional state of the animals, and the lack of predation pressure in the laboratory.

It may be advantageous to have one animal in the family group that transports the

infants whilst the other group members can travel unhindered around the territory. This behaviour would allow time for foraging whilst not carrying the infants, and also afford protection and care for the infants. Locke-Haydon (1984c) stressed the importance of carrying by the caregivers which enables the infants to keep up with the family group, to be protected and cared for. Division of labour within the family group allows for the reproductive strategy seen in the marmosets. Scanlon (pers. comm.), also noted that the groups with infants in them tended to remain together to a greater extent than those groups with no infants. This observation supports the concept that all the family members have a role in caring for the infants.

A general observation from the study was that the older siblings were often aggressive toward the parents whilst carrying their offspring. There are two possible explanations for the behaviour: either the aggression may be a form of competition to gain access to the infants, or the older siblings are soliciting some form of parental care directed towards themselves. I have sometimes observed the siblings take the infants from a parent and then immediately try to rub them off, in some cases quite vigorously. Snowden & Suomi (1982) have postulated that the siblings may be interested in the infants, but that once they have them on their back, they find them uncomfortable, and so try to dislodge them. Thus the siblings may be trying to maximise their own care, in competition with the parents preference for carrying the new infants (Trivers '74). Trivers' (1974) parent-infant conflict, argues that the parent has been selected to invest in the infant to maximise its own reproductive output. The conflict arises because the infant's own reproductive success is maximised by obtaining more care than the parent is prepared to give. The intensity of this conflict normally increases over the period of parental care. Providing more care may result in increased survival of the offspring, but at the expense of

investment in other offspring. Trivers proposes that the weaning conflict between mother and offspring, and indeed conflict before weaning will be less, if successive sets of infants are fathered by the same male. In other primates such as langurs and baboons, where paternity is uncertain, conflict may be seen to last for several weeks.

Although there may be general care-giving patterns in the callitrichids (Ingram 1977), there is also much variation both between family groups and between the species (Box 1977). *Callimico*, *Callicebus*, *Aotus* and *Saimiri* are also small New World primates. They differ from callitrichids in the respect that they produce singleton litters. However, with the exception of *Saimiri*, they are monogamous and exhibit biparental care, which Wright (1984) suggests are primitive traits. *Saimiri* exist in polygamous family groups, and infant care takes the form of 'aunting' by other females in the troupe. Kleiman (1977) proposed that the variation seen in the role of the male in caring for the infants may be related to the maternal-offspring weight ratio at birth. An increase in the weight ratio would result in a greater degree of paternal care, with the male beginning to help carry the offspring earlier. In *Cebus* and *Alouatta* the females generally do the carrying, and the single infants are small, relative to the mother, at birth. Some alloparenting may occur in *Cebus* (Welker et al. 1987). In monogamous family groups in *Alouatta* (Bolin 1981), there may be some male care of the infants showing the enormous potential for paternal care that may become apparent if the opportunity arises.

To conclude therefore, the organisation of carrying behaviour can be interpreted as an adaptation to the extreme burdens that are placed upon the caregivers whilst they are carrying infants. In this way, the infants are constantly cared

for in the early period of their lives, and that the necessary protection is provided.

4.2 FURTHER ANALYSIS AND FUTURE PROJECTS.

Further studies could be carried out looking at the overall rates of activity in families that had no infants within them. This would allow testing of the prediction that overall rates of activity would be greater for families with no infants.

Further studies could be carried out to assess the postural changes in the caregivers as they carry their infants. One way to examine these changes would be to video the caregiver whilst it is carrying the infants and moving.

In this way, it would also be possible to look at the way the infants are positioned on the caregiver. Kohda (1975) noted that New and Old world species carried their infants in different ways, and that there were also differences in the caregiving behaviour of the New and Old world primates that may have been related to the way in which the infants were carried.

APPENDIX 1

The mean mass of mother and infants during the first twenty weeks of the infants life used in Fig 1.1.

WEEKS	MOTHER (g) (n = 8)	INFANTS(g) (n = 18)	MALE (g) (n = 8)	FEMALE (g) (n = 10)
1	393.3	29.8	29.8	29.8
2	392.2	34.2	33.3	34.9
3	396.3	41.3	40.6	41.8
4	405.4	48.5	47.8	49.0
5	408.1	57.2	54.6	59.6
6	409.9	65.7	63.1	68.1
7	416.2	75.4	72.7	77.8
8	411.3	84.7	82.5	86.7
9	408.6	97.4	94.2	14.4
10	405.1	110.8	106.3	109.8
11	411.0	123.4	121.9	127.7
12	403.1	131.3	130.9	131.5
13	401.8	141.7	141.5	131.5
14	405.9	148.8	148.7	148.9
15	409.3	159.1	158.6	159.5
16	415.5	166.1	166.3	165.9
17	424.1	176.2	177.4	175.2
18	443.7	182.5	182.4	182.6
19	445.8	192.9	194.5	191.7
20	-	199.5	200.2	198.8

Mean mass changes were collected for eight females. There were eighteen infants, of which ten were female and eight were male.

There were no significant differences between the rate of growth of male and female infants.

APPENDIX 2

Appendix 2.1 Log Likelihood Ratio test, to examine whether there is a preference for caregivers to be in state 0 or state 2.

$$-2 \left\{ N_{01} \log \left[\frac{(N_{01} + N_{12})}{(2\beta_0 + \beta_1)} * \frac{2\beta_0}{N_{01}} \right] + N_{12} \log \left[\frac{(N_{01} + N_{12})}{(2\beta_0 + \beta_1)} * \frac{\beta_1}{N_{01}} \right] \right. \\ \left. + N_{10} \log \left[\frac{(N_{10} + N_{21})}{(\beta_1 + 2\beta_2)} * \frac{\beta_1}{N_{10}} \right] + N_{21} \log \left[\frac{(N_{10} + N_{21})}{(\beta_1 + 2\beta_2)} * \frac{2\beta_2}{N_{21}} \right] \right\}$$

N_{01} - No. of climb-ons/pick-ups in state 0

N_{12} - No. of climb-ons/pick-ups in state 1

N_{21} - No. of rub-off/climb-offs in state 2

N_{10} -No. of rub-off/climb-offs in state 1

β_0 - Time spent in state 0

β_1 - Time spent in state 1

β_2 - Time spent in state 2

The calculated statistic value, is compared with the χ^2 Table of values at two degrees of freedom.

The log likelihood ratio tests the null hypothesis that the 3-state process is the sum of two independent 2-state random processes, one for each offspring.

Under the null hypothesis, the parent treats each of the two infants

independently, picking up or putting down each one regardless of whether or not the other is being carried at the time. An assumption is made that the caregiver must step from one state to another, and cannot jump two states. For example there is a step from state 0 to 1, and state 1 to 2; but can't go from state 0 to 2.

The intermediate state 1 may be very brief.

Appendix 2.2

Statistical test to examine rate of movement of infants whilst the caregivers in each of state 0, 1 or 2.

$$\hat{\lambda}_0 = \frac{\lambda_0}{2\beta_0} \quad = \text{rate of movement/hr.}$$

$$\hat{\lambda}_1 = \frac{\lambda_1}{\beta_1} \quad = \text{rate of movement/hr.}$$

$$\text{S.E.} = \sqrt{\frac{\lambda_0}{4(\beta_0)^2} + \frac{\lambda_1}{(\beta_1)^2}}$$

$$Z = \frac{\hat{\lambda}_1 - \hat{\lambda}_0}{\text{S.E.}}$$

λ_0 = no. of pick-ups/climb-ons in state 0

λ_1 = no. of pick-ups/climb-ons in state 1

β_0 = time spent in state 0

β_1 = time spent in state 1

The calculated statistic is compared with the Z statistic table of values.

The Standard Error of rates of movement are calculated for individuals, as it is assumed that they are random processes. The t-test is not used because the data are not normal; the sample size is low; and S.E. is calculated for the pooled individual data, which is not random.

Appendix 2.3

Statistical test to examine rate of movement of infants whilst the caregivers in each of state 0, 1 or 2.

$$\hat{\mu}_2 = \frac{\mu_2}{2\beta_2} \quad = \text{rate of movement/hr.}$$

$$\hat{\mu}_1 = \frac{\mu_1}{\beta_1} \quad = \text{rate of movement/hr.}$$

$$\text{S.E.} = \sqrt{\frac{\mu_2}{4(\beta_2)^2} + \frac{\mu_1}{(\beta_1)^2}}$$

$$Z = \frac{\hat{\mu}_2 - \hat{\mu}_1}{\text{S.E.}}$$

μ_2 = no. of rub-off/climb-offs in state 2

μ_1 = no. of rib-off/climb-offs in state 1

β_2 = time spent in state 2

β_1 = time spent in state 1

The calculated statistic is compared with the Z statistic table of values.

The Standard Error of rates of movement are calculated for individuals, as it is assumed that they are random processes. The t-test is not used because the data are not normal; the sample size is low; and S.E. is calculated for the pooled individual data, which is not random.

These statistics were suggested and provided by Dr. K. McConway, of the statistics department at the Open University.

APPENDIX 3

Programme written in APPLE BASIC, used to collect the data during the observation sessions, with facility to correct any errors made during the observation period, before the data were stored on disk.

```
10 REM THIS PROG RECORDS ON 2 DRIVES
20 REM IF 0 IS PRESSED A BACKUP FILE
30 REM CALLED DATABACK IS PRODUCED
40 REM WHILST RECORDING
50 FOR X = 2 TO 1 STEP - 1
60 D$ = CHR$(4): PRINT D$;"OPEN DUMMY,D";X: PRINT D$;"CLOSE DUMMY"
70 NEXT X
80 PRINT :Y = 1988
90 PRINT "FIONASREC THE RECORDING AND EDITING PROGRAM FOR TWO
DRIVES"
100 PRINT
110 INPUT "ENTER THE SESSION NUMBER ";SN
120 PRINT
130 INPUT "ENTER SUB-SESSION NUMBER ";SB
140 PRINT
150 INPUT "WHAT AGE ARE THE INFANTS? ";AS
160 PRINT
170 INPUT "WHAT IS THE SUBJECT'S CODE NUMBER?
MOTHER=1,FATHER=2,SIB1 MALE=3,SIB1 FEMALE=4,SIB2 MALE=5,SIB2
FEMALE=6 ";CN
180 PRINT
190 PRINT "SEX OF INFANT 1? UNKNOWN = 0, MALE = 1": INPUT "FEMALE = 2
";SS
200 PRINT "SEX OF INFANT 2? UNKNOWN = 0, MALE = 1": INPUT "FEMALE = 2
";SY
210 PRINT : PRINT "OBSERVER'S CODE NUMBER ?": PRINT
220 PRINT "1. FIONA": PRINT "2. ROBERT": PRINT "3. NEIL": INPUT ID
230 PRINT
240 INPUT "PRESS RETURN KEY TO MARK BEGINNING OF SESSION";A$
250 GOSUB 1090
260 GOSUB 600
270 HOME : PRINT "START NOW"
280 DIM A(4000)
290 A(1) = D:A(2) = MO
300 A(3) = Y
310 A(4) = (H * 3600) + (M * 130) + S
```

```

320 A(5) = SN:A(6) = AS:A(7) = CN
330 A(8) = SS:A(9) = ID:A(10) = SB:A(13) = SY
340 A(14) = H:A(15) = M:A(16) = S
350 I = 21
360 GOTO 410
370 FOR Z = 1 TO 10
380 SOUND = PEEK ( - 16336)
390 NEXT
400 GOTO 460
410 HOME
420 PRINT
430 PRINT "NEXT BEHAVIOUR WILL BE ENTERED"
440 PRINT "IN ARRAY POSITION ";I:C$ = B$
450 GET B$: GOTO 370
460 HOME : IF B$ = CHR$ (48) GOTO 2540
470 IF B$ < > CHR$ (32) GOTO 500
480 I = I - 2: GET B$:A(I) = ASC (B$): PRINT B$: PRINT
490 I = I + 2: GOTO 680
500 IF B$ = CHR$ (33) GOTO 1200
510 A(I) = ASC (B$)
520 HOME
530 PRINT B$
540 I = I + 1
550 X$ = CHR$ (13)
560 PRINT X$
570 GOSUB 1090
580 GOSUB 600
590 GOTO 660
600 HOUR$ = MID$ (T$,7,2):H = VAL (HOUR$)
610 MIN$ = MID$ (T$,10,2):M = VAL (MIN$)
620 SEC$ = RIGHT$ (T$,6):S = VAL (SEC$)
630 DAY$ = MID$ (T$,4,2):D = VAL (DAY$)
640 M$ = LEFT$ (T$,2):MO = VAL (M$)
650 RETURN
660 A(I) = (H * 3600) + (M * 130) + S
670 I = I + 1
680 IF I = 3499 GOTO 720
690 IF I = 3899 GOTO 770
700 IF I = 3999 GOTO 840
710 GOTO 430
720 FOR Z = 1 TO 100
730 SOUND = PEEK ( - 16336)
740 NEXT Z

```

```

750 PRINT "ONLY 500 SPACES LEFT"
760 GOTO 430
770 B = - 16336
780 HOME
790 PRINT "ONLY 100 SPACES LEFT!!"
800 FOR Z = 1 TO 100
810 SOUND = PEEK (B) - PEEK (B) - PEEK (B)
820 NEXT Z
830 GOTO 430
840 HOME : INVERSE : FLASH
850 PRINT "STOP!!!"
860 NORMAL
870 FOR Z = 1 TO 300
880 SOUND = PEEK ( - 16336)
890 NEXT Z
900 INPUT "ENTER *";A$
910 A(I) = ASC (A$)
920 X$ = CHR$ (13)
930 PRINT X$
940 GOSUB 1090
950 GOSUB 600
960 A(17) = H:A(18) = M:A(19) = S
970 I = I + 1
980 A(I) = (H * 3600) + (M * 130) + S
990 C = A(I):Y9 = A(4)
1000 PRINT
1010 PRINT "SESSION ENDED AT ";RIGHT$ (T$,12)
1020 PRINT
1030 PRINT "NUMBER OF ENTRIES IN ARRAY = ";I
1040 A(11) = I
1050 PRINT : PRINT
1060 PRINT : PRINT
1070 INPUT "TO CONTINUE PRESS RETURN ";A$
1080 GOTO 1240
1090 SLOT = 4
1100 D$ = ""
1110 PRINT D$;"NOMON C,I,O"
1120 PRINT D$;"IN*";SLOT
1130 PRINT D$;"PR*";SLOT
1140 INPUT " ";T$
1150 PRINT D$;"IN*0"
1160 PRINT D$;"PR*0"

```

```

1170 RETURN
1180 END
1190 PRINT "WHICH OF THE FOLLOWING DO YOU WANT?"
1200 A(I) = ASC (B$)
1210 X$ = CHR$ (13)
1220 PRINT X$
1230 GOTO 940
1240 HOME
1250 INPUT "TO TRANSFER DATA TO DISK PRESS RETURN ";A$
1260 I = A(11)
1270 GOTO 1310
1280 PRINT
1290 INPUT "TYPING ERROR. TRY AGAIN ";C$
1300 GOTO 1270
1310 PRINT : PRINT
1320 INPUT "ENTER FILE NAME ";P$
1330 D$ = ""
1340 FOR X = 1 TO 2
1350 PRINT D$;"OPEN ";P$;"D"X",V1"
1360 FOR K = 1 TO I
1370 PRINT D$;"WRITE ";P$
1380 PRINT A(K)
1390 NEXT K
1400 PRINT D$;"CLOSE ";P$
1410 PRINT
1420 NEXT X
1430 PRINT D$;"OPEN DUMMY": PRINT D$;"WRITE DUMMY": PRINT P$: PRINT
D$;"CLOSE DUMMY"
1440 INPUT "IF YOU WANT TO STORE DATA AGAIN PRESS Y, IF NOT PRESS N
";A$
1450 PRINT
1460 IF A$ = "Y" GOTO 1320
1470 PRINT : PRINT : FLASH
1480 PRINT "GOING TO EDIT PROGRAM"
1490 PRINT : NORMAL
1500 CLEAR
1510 D$ = CHR$ (4): PRINT D$;"OPEN DUMMY": PRINT D$;"READ DUMMY":
INPUT P$: PRINT D$;"CLOSE DUMMY"
1520 PRINT "EDIT "P$" ?"
1530 INPUT A$: IF A$ = "Y" GOTO 1550
1540 INPUT "ENTER FILE NAME ";P$
1550 PRINT : PRINT D$;"OPEN";P$
1560 PRINT D$;"POSITION";P$;"R10": PRINT D$;"READ";P$: INPUT B: PRINT

```

```

D$;"CLOSE";P$
1570 DIM A(B + 30): PRINT D$;"OPEN ";P$: PRINT : PRINT D$;"READ ";P$: FOR
K = 1 TO B: INPUT A(K): NEXT : PRINT D$;"CLOSE ";P$
1580 PRINT D$;"PR#1": PRINT : PRINT : PRINT P$: PRINT
1590 PRINT "RECORDED ON "A(1)"/"A(2)"/"A(3);
1600 PRINT " AT "A(14)":"A(15)":"A(16);
1610 PRINT " BY OBSERVER "A(9)
1620 PRINT "SESSION ENDED AT "A(17)":"A(18)":"A(19): PRINT
1630 PRINT "SUBJECT "A(7)
1640 PRINT " SEX OF INFANT 1= "A(8)" SEX OF INFANT 2= "A(13)
1650 PRINT "AGE OF INFANTS= "A(6)" WEEK(S)"
1660 PRINT
1670 GOSUB 1690
1680 GOTO 1750
1690 FOR K = 21 TO B - 1 STEP 2
1700 IF A(K) > 26 GOTO 1720
1710 X = A(K) + 64: PRINT "("K;" ) CONTROL "; CHR$(X); " ";A(K + 1); " ";GOTO
1730
1720 PRINT "("K;" ) CHR$(A(K)); " ";A(K + 1); " "
1730 NEXT
1740 RETURN
1750 PRINT : PRINT D$;"PR#0": PRINT : PRINT
1760 HOME : PRINT : PRINT "SELECT ONE OF THE FOLLOWING"
1770 PRINT : PRINT "1. INSERT OR SUBSTITUTE CODES": PRINT " CONTROL U, H
OR M"
1780 PRINT "2. SUBSTITUTE EXISTING BEHAVIOUR BY ": PRINT " ANOTHER"
1790 PRINT "3. DELETE EXISTING BEHAVIOUR"
1800 PRINT "4. INSERT ADDITIONAL BEHAVIOUR"
1810 PRINT "5. ACCEPT FILE AS IT STANDS"
1820 INPUT A
1830 IF A > 5 GOTO 1760
1840 ON A GOTO 1850,1980,2050,2070,2220
1850 HOME : PRINT : PRINT "ENTER CONTROL CODE NUMBER"
1860 PRINT : PRINT " 8. CONTROL H"
1870 PRINT "13. CONTROL M"
1880 PRINT "21. CONTROL U"
1890 INPUT CC
1900 IF CC < > 8 AND CC < > 13 AND CC < > 21 GOTO 1850
1910 PRINT : PRINT "ENTER 1 TO SUBSTITUTE, 2 TO INSERT CODE"
1920 INPUT FL
1930 ON FL GOTO 1940,1960
1940 INPUT "ENTER CELL NO TO BE CHANGED ";K

```

```

1950 A(K) = CC: GOTO 2020
1960 INPUT "ENTER CELL NO INTO WHICH NEW CODE IS TO BE INSERTED ";K
1970 B$ = CHR$(CC): GOTO 2090
1980 INPUT "ENTER CELL NO. TO BE CHANGED ";K
1990 PRINT "ENTER NEW CODE FOR CELL ";K
2000 INPUT B$
2010 A(K) = ASC (B$)
2020 PRINT : INPUT "DO YOU WANT TO CHANGE OTHER CODES? Y OR N? ";A$
2030 IF A$ < > "Y" AND A$ < > "N" GOTO 2490
2040 GOTO 2520
2050 INPUT "ENTER CELL NO. TO BE DELETED ";K
2060 A(K) = 45: GOTO 2020
2070 INPUT "ENTER CELL NO. INTO WHICH NEW CODE IS TO BE INSERTED ";K
2080 PRINT : PRINT : INPUT "ENTER NEW CODE TO BE INSERTED ";B$ 2090
A(11) = A(11) + 2
2100 B = B + 2
2110 S3 = A(K):S4 = A(K + 1):S1 = ASC (B$):S2 = A(K - 1)
2120 FOR X = K TO B - 1 STEP 2
2130 A(X) = S1:A(X + 1) = S2:S1 = S3:S2 = S4
2140 S3 = A(X + 2):S4 = A(X + 3): NEXT
2150 A(X + 4) = S3:A(X + 5) = S4: GOTO 2020
2160 HOME
2170 PRINT "INSPECT EDITED FILE"
2180 PRINT D$;"PR#1"
2190 PRINT : PRINT
2200 PRINT "EDITED ";P$
2210 GOSUB 1690
2220 PRINT
2230 PRINT D$;"PR#0"
2240 HOME : INPUT "SATISFIED? Y OR N? ";A$
2250 PRINT
2260 IF A$ = "N" GOTO 1750
2270 PRINT "IS EDITED FILE "P$ + "E"
2280 INPUT A$: IF A$ = "N" GOTO 2300
2290 E$ = P$ + "E": GOTO 2310
2300 PRINT : INPUT "ENTER NAME OF EDITED FILE. ";E$
2310 INPUT "PRESS RETURN TO STORE DATA ON DISK ";A$
2320 PRINT D$;"OPEN ";E$
2330 PRINT D$;"WRITE ";E$
2340 FOR K = 1 TO B
2350 PRINT A(K)
2360 NEXT K
2370 PRINT D$;"CLOSE ";E$

```

```

2380 PRINT : INPUT "DO YOU WANT TO STORE DATA AGAIN? Y OR N? ";A$
2390 IF A$ = "Y" GOTO 2300
2400 PRINT D$;"LOCK "E$: PRINT D$;"LOCK "P$
2410 PRINT : INPUT "CATALOG? Y OR N? ";A$
2420 IF A$ = "N" GOTO 2440
2430 PRINT D$;"CATALOG": PRINT
2440 PRINT : PRINT "PRESS ANY KEY TO CONTINUE": GET A$
2450 PRINT : PRINT D$;"CATALOG D1": PRINT : PRINT "DO YOU WISH TO
DELETE ";P$;" ON THIS DISC? ": INPUT A$
2460 IF A$ < > "Y" GOTO 2480
2470 PRINT D$;"DELETE ";P$
2480 CLEAR : HOME : GOTO 50
2490 HOME : PRINT : PRINT : PRINT : PRINT : INVERSE : FLASH : PRINT "BERK -
YOU'RE NOT CONCENTRATING": NORMAL
2500 FOR Z = 1 TO 15:SOUND = PEEK ( - 16336): NEXT
2510 GOTO 2020
2520 IF A$ = "Y" THEN PRINT : PRINT : GOTO 1760
2530 IF A$ = "N" GOTO 2160
2540 A(I) = ASC (B$):X$ = CHR$ (13): PRINT X$
2550 GOSUB 1090: GOSUB 600
2560 A(17) = H:A(18) = M:A(19) = S
2570 IN = I + 1
2580 A(IN) = (H * 3600) + (M * 130) + S
2590 C = A(IN):Y9 = A(4)
2600 A(11) = IN
2610 PRINT D$;"OPEN DATABACK"
2620 FOR K = 1 TO IN
2630 PRINT D$;"WRITE DATABACK"
2640 PRINT A(K)
2650 NEXT K
2660 PRINT D$;"CLOSE DATABACK"
2670 GOTO 470

```


APPENDIX 4

Programme written in APPLE BASIC, used to analyse the data that had been collected and stored on disk, during observation sessions.

```
10 REM ANALYSE RESULTS
20 REM PROGRAM TO ANALYSE DATA FROM FOUR SESSIONS, OVER A PERIOD
  OF FOUR WEEKS USING RECORDING PROGRAMME
30 D$ = CHR$(4): PRINT D$;"NOMON,C,I,O"
40 DIM A(76): DIM C(4000)
50 HOME : PRINT : PRINT : INPUT "ENTER THE WEEK'S SUBJECT ORDER E.G.
  MXFY (N.B. PLEASE NO SPACES) ";PO$
60 PRINT : INPUT "ENTER THE CAGE NO ";CG$
70 PRINT : INPUT "ENTER THE TREATMENT NO ";T$
80 PRINT : INPUT "ENTER THE WEEKS COVERED, E.G. 1-2 OR 5-6 ";WK$
90 PRINT : INPUT "IS THIS DATA CORRECT? (Y OR N) ";M1$: IF M1$ = "N" THEN
  GOTO 50
100 Q$ = CG$ + " WK" + WK$ + " T" + T$
110 PRINT : PRINT : INPUT "DO YOU WANT A PRINTED OUTPUT? Y OR N ";B$
120 PRINT : PRINT : INPUT "DO YOU WANT AN ARRAY A(1)-A(76) WRITTEN
  AND APPENDED TO A FILE ON DISC? ";C$
130 IF C$ = "N" GOTO 150
140 PRINT : PRINT : INPUT "ENTER FILE NAME ";E$
150 REM LINES 50 TO 190 ADD THE SESSION NO TO THE MAIN FILE NAME AND
  SO ALLOW SESSIONS TO BE ANALYSED IN TURN. SN STANDS FOR SESSION
160 PRINT : PRINT : INPUT "ANY SESSIONS MISSING? Y OR N ";A$
170 I = 1
180 IF A$ = "N" GOTO 220
190 PRINT : PRINT : INPUT "ENTER MISSING SESSION NUMBERS. PRESS RETURN
  AFTER EACH. PRESS 99 WHEN FINISHED. ";A
200 D(I) = A: IF A = 99 GOTO 240
210 I = I + 1: GOTO 190
220 D(I) = 99
230 IF B$ = "N" GOTO 250
240 PRINT D$;"PR#1"
250 FOR SN = 1 TO 4
260 NC = 0
270 P$ = MID$(PO$,SN,1) + Q$
280 I = 1
290 IF SN < > D(I) GOTO 310
300 PRINT : PRINT "SESSION ";SN;" MISSING": GOTO 2050
310 IF D(I) = 99 GOTO 330
```

```

320 I = I + 1: GOTO 290
330 P$ = P$ + " S0" + STR$ (SN) + "E"
340 PRINT D$;"OPEN ";P$: PRINT D$;"POSITION ";P$;"R10"
350 PRINT D$;"READ";P$: INPUT B
360 PRINT D$;"CLOSE";P$
370 PRINT D$;"OPEN ";P$: PRINT D$;"READ";P$:
380 FOR K = 1 TO B: INPUT C(K): NEXT
390 PRINT D$;"CLOSE";P$
400 K = 21: SW = 0
410 PRINT : PRINT P$
420 REM NEXT SECTION SETS UP DIFFERENT WAYS OF DEALING WITH CODES
THAT REPRESENT ONGOING STATES AT ONSET OF SESSION AND OTHER CODES
430 IF C(K) < > 45 GOTO 450: REM CHECK FOR - AS FIRST CHARACTER
440 K = K + 2: GOTO 430
450 IF C(K) < > ASC ("X") GOTO 620
460 K = K + 2: C(K + 1) = C(4): REM C4 IS THE SESSION STARTING TIME
470 IF C(K) < > ASC ("X") GOTO 490
480 SW = 1: GOTO 630
490 L = K
500 REM SEARCH FOR START KEYS BETWEEN X AND X
510 GOSUB 3110: IF FL = 1 OR C(L) = 45 GOTO 630: REM CHECK FOR WRONG
FOCAL ANIMAL KEY AND DELETE BETWEEN XX
520 IF C(L) = 85 OR C(L) = 21 GOTO 1390: REM U AND CONTROL U
530 IF C(L) = 73 OR C(L) = 9 GOTO 1480: REM I AND CONTROL I
540 IF C(L) = 79 OR C(L) = 15 GOTO 1560: REM O AND CONTROL O
550 IF C(L) = 80 OR C(L) = 16 GOTO 1640: REM P AND CONTROL P
560 IF C(L) = 81 OR C(L) = 17 GOTO 1730: REM Q AND CONTROL Q
570 IF C(L) = 87 OR C(L) = 23 GOTO 1810: REM W AND CONTROL W
580 IF C(L) = 69 OR C(L) = 5 GOTO 1890: REM E AND CONTROL E
590 IF C(L) = 82 OR C(L) = 18 GOTO 1970: REM R AND CONTROL R
600 PRINT : PRINT "SESSION ";SN;" RECORD ";K;" ILEGAL CODE BETWEEN X X"
610 GOTO 630
620 K = 19: SW = 1
630 IF SW = 0 GOTO 460: REM SW IS A SWITCH WHICH IS CHANGED FROM 0 TO
1 WHEN INITIAL STATES HAVE BEEN RECORDED
640 K = K + 2: IF C(K) = ASC ("I") GOTO 2080
650 PRINT D$;"PR#0": HOME : PRINT "RECORD ";K: PRINT D$;"PR#1"
660 REM SELECTION OF APPROPRIATE ANALYSIS FOR BEHAVIOUR CODE
RECORDED
670 GOSUB 3110: IF FL = 1 GOTO 630
680 REM REJECTIONS INFANT 1
690 IF C(K) = 66 THEN A(0) = A(0) + 1: GOTO 1250
700 IF C(K) = 78 THEN A(1) = A(1) + 1: GOTO 1250

```

```

710 IF C(K) = 77 THEN A(2) = A(2) + 1: GOTO 1250
720 IF C(K) = 44 THEN A(3) = A(3) + 1: GOTO 1250
730 REM REJECTIONS INFANT 2
740 IF C(K) = 90 THEN A(4) = A(4) + 1: GOTO 1250
750 IF C(K) = 88 THEN A(5) = A(5) + 1: GOTO 1250
760 IF C(K) = 67 THEN A(6) = A(6) + 1: GOTO 1250
770 IF C(K) = 86 THEN A(7) = A(7) + 1: GOTO 1250
780 REM NO OF DISTRESS CALLS INFANT 1
790 IF C(K) = 89 THEN A(9) = A(9) + 1: A(11) = A(11) + 1: GOTO 1270
800 REM NO OF DISTRESS CALLS INFANT 2
810 IF C(K) = 84 THEN A(10) = A(10) + 1: A(11) = A(11) + 1: GOTO 1320
820 REM INFANT 1 CLIMBS ON
830 IF C(K) = 85 THEN A(15) = A(15) + 1: A(23) = A(23) + 1: GOTO 1390
840 IF C(K) = 73 THEN A(16) = A(16) + 1: A(23) = A(23) + 1: GOTO 1480
850 IF C(K) = 79 THEN A(17) = A(17) + 1: A(23) = A(23) + 1: GOTO 1560
860 IF C(K) = 80 THEN A(18) = A(18) + 1: A(23) = A(23) + 1: GOTO 1640
870 REM INFANT 2 CLIMBS ON
880 IF C(K) = 81 THEN A(19) = A(19) + 1: A(23) = A(23) + 1: GOTO 1730
890 IF C(K) = 87 THEN A(20) = A(20) + 1: A(23) = A(23) + 1: GOTO 1810
900 IF C(K) = 69 THEN A(21) = A(21) + 1: A(23) = A(23) + 1: GOTO 1890
910 IF C(K) = 82 THEN A(22) = A(22) + 1: A(23) = A(23) + 1: GOTO 1970
920 REM INFANT 1 PICKED UP
930 IF C(K) = 21 THEN A(24) = A(24) + 1: A(32) = A(32) + 1: GOTO 1390
940 IF C(K) = 9 THEN A(25) = A(25) + 1: A(32) = A(32) + 1: GOTO 1480
950 IF C(K) = 15 THEN A(26) = A(26) + 1: A(32) = A(32) + 1: GOTO 1560
960 IF C(K) = 16 THEN A(27) = A(27) + 1: A(32) = A(32) + 1: GOTO 1640
970 REM INFANT 2 PICKED UP
980 IF C(K) = 17 THEN A(28) = A(28) + 1: A(32) = A(32) + 1: GOTO 1730
990 IF C(K) = 23 THEN A(29) = A(29) + 1: A(32) = A(32) + 1: GOTO 1810
1000 IF C(K) = 5 THEN A(30) = A(30) + 1: A(32) = A(32) + 1: GOTO 1890
1010 IF C(K) = 18 THEN A(31) = A(31) + 1: A(32) = A(32) + 1: GOTO 1970
1020 REM INFANT 1 CLIMBS OFF
1030 IF C(K) = 72 THEN A(33) = A(33) + 1: A(41) = A(41) + 1: NC = NC - 1: GOTO
630
1040 IF C(K) = 74 THEN A(34) = A(34) + 1: A(41) = A(41) + 1: GOTO 630
1050 IF C(K) = 75 THEN A(35) = A(35) + 1: A(41) = A(41) + 1: GOTO 630
1060 IF C(K) = 76 THEN A(36) = A(36) + 1: A(41) = A(41) + 1: GOTO 630
1070 REM INFANT 2 CLIMBS OFF
1080 IF C(K) = 65 THEN A(37) = A(37) + 1: A(41) = A(41) + 1: NC = NC - 1: GOTO
630
1090 IF C(K) = 83 THEN A(38) = A(38) + 1: A(41) = A(41) + 1: GOTO 630
1100 IF C(K) = 68 THEN A(39) = A(39) + 1: A(41) = A(41) + 1: GOTO 630

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1110 IF C(K) = 70 THEN A(40) = A(40) + 1:A(41) = A(41) + 1: GOTO 630
1120 REM INFANT 1 RUBBED OFF
1130 IF C(K) = 8 THEN A(42) = A(42) + 1:A(50) = A(50) + 1:NC = NC - 1: GOTO
630
1140 IF C(K) = 10 THEN A(43) = A(43) + 1:A(50) = A(50) + 1: GOTO 630
1150 IF C(K) = 11 THEN A(44) = A(44) + 1:A(50) = A(50) + 1: GOTO 630
1160 IF C(K) = 12 THEN A(45) = A(45) + 1:A(50) = A(50) + 1: GOTO 630
1170 REM INFANT 2 RUBBED OFF
1180 IF C(K) = 1 THEN A(46) = A(46) + 1:A(50) = A(50) + 1:NC = NC - 1: GOTO
630
1190 IF C(K) = 19 THEN A(47) = A(47) + 1:A(50) = A(50) + 1: GOTO 630
1200 IF C(K) = 4 THEN A(48) = A(48) + 1:A(50) = A(50) + 1: GOTO 630
1210 IF C(K) = 6 THEN A(49) = A(49) + 1:A(50) = A(50) + 1: GOTO 630
1220 IF C(K) = 55 GOTO 2040
1230 IF C(K) = 56 GOTO 2060
1240 GOTO 630
1250 A(8) = A(8) + 1: GOTO 630
1260 REM DURATION OF CALLS INFANT 1
1270 L = K + 2
1280 IF C(L) = 33 OR C(L) = 25 GOTO 1300
1290 L = L + 2: GOTO 1280
1300 A(12) = A(12) + C(L + 1) - C(K + 1):A(14) = A(14) + C(L + 1) - C(K + 1):
GOTO 630
1310 REM DURATION CALLS INFANT 2
1320 L = K + 2
1330 IF C(L) = 33 OR C(L) = 20 GOTO 1350
1340 L = L + 2: GOTO 1330
1350 A(13) = A(13) + C(L + 1) - C(K + 1):A(14) = A(14) + C(L + 1) - C(K + 1):
GOTO 630
1360 PRINT : PRINT "SESSION ";SN;"RECORD ";K;"DISTRESS CALL END CODE
MISSING ": GOTO 490
1370 REM TIME ON CAREGIVERS INFANT 1
1380 REM TIME ON MOTHER
1390 L = K + 2:NC = NC + 1
1400 IF C(L) < > 33 AND C(L) < > 8 AND C(L) < > 89 AND C(L) < > 25 AND C(L) <
> 72 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
1420
1410 GOTO 1430
1420 IF C(L) < > 84 AND C(L) < > 20 AND C(L) < > 65 AND C(L) < > 1 AND C(L) <
> 17 AND C(L) < > 81 AND C(L) < > 90 GOTO 1450
1430 IF C(L) = 33 OR C(L) = 72 OR C(L) = 8 GOTO 1470
1440 L = L + 2: GOTO 1400
1450 PRINT : PRINT "SESSION ";SN;"RECORD ";K;" OFF CODE MISSING "

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1460 GOTO 630: REM PRINT OFF
1470 A(51) = A(51) + C(L + 1) - C(K + 1):A(59) = A(59) + C(L + 1) - C(K +
1):A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
1480 L = K + 2
1490 IF C(L) < > 33 AND C(L) < > 74 AND C(L) < > 89 AND C(L) < > 25 AND C(L)
< > 10 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
1510
1500 GOTO 1520
1510 IF C(L) < > 84 AND C(L) < > 20 AND C(L) < > 83 AND C(L) < > 19 AND C(L)
< > 23 AND C(L) < > 87 AND C(L) < > 88 GOTO 1450
1520 IF C(L) = 33 OR C(L) = 74 OR C(L) = 10 GOTO 1540
1530 L = L + 2: GOTO 1490
1540 A(52) = A(52) + C(L + 1) - C(K + 1):A(60) = A(60) + C(L + 1) - C(K +
1):A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
1550 REM TIME ON SIB1
1560 L = K + 2
1570 IF C(L) < > 33 AND C(L) < > 75 AND C(L) < > 89 AND C(L) < > 25 AND C(L)
< > 11 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
1590
1580 GOTO 1600
1590 IF C(L) < > 84 AND C(L) < > 20 AND C(L) < > 68 AND C(L) < > 4 AND C(L) <
> 5 AND C(L) < > 69 AND C(L) < > 67 GOTO 1450
1600 IF C(L) = 33 OR C(L) = 75 OR C(L) = 11 GOTO 1620
1610 L = L + 2: GOTO 1570
1620 A(53) = A(53) + C(L + 1) - C(K + 1):A(61) = A(61) + C(L + 1) - C(K +
1):A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
1630 REM TIME ON SIB2
1640 L = K + 2
1650 IF C(L) < > 33 AND C(L) < > 76 AND C(L) < > 89 AND C(L) < > 25 AND C(L)
< > 12 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
1670
1660 GOTO 1680
1670 IF C(L) < > 84 AND C(L) < > 20 AND C(L) < > 6 AND C(L) < > 70 AND C(L) <
> 18 AND C(L) < > 82 AND C(L) < > 86 GOTO 1450
1680 IF C(L) = 33 OR C(L) = 76 OR C(L) = 12 GOTO 1700
1690 L = L + 2: GOTO 1650
1700 A(54) = A(54) + C(L + 1) - C(K + 1):A(62) = A(62) + C(L + 1) - C(K +
1):A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
1710 REM TIME ON CARE GIVERS INFANT 2
1720 REM TIME ON MOTHER
1730 L = K + 2: NC = NC + 1
1740 IF C(L) < > 33 AND C(L) < > 65 AND C(L) < > 84 AND C(L) < > 20 AND C(L)

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< > 1 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
1760
1750 GOTO 1770
1760 IF C(L) < > 25 AND C(L) < > 89 AND C(L) < > 21 AND C(L) < > 85 AND C(L)
< > 8 AND C(L) < > 72 AND C(L) < > 66 GOTO 1450
1770 IF C(L) = 33 OR C(L) = 65 OR C(L) = 1 GOTO 1790
1780 L = L + 2: GOTO 1740
1790 A(55) = A(55) + C(L + 1) - C(K + 1): A(59) = A(59) + C(L + 1) - C(K +
1): A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
1800 REM TIME ON FATHER
1810 L = K + 2
1820 IF C(L) < > 33 AND C(L) < > 83 AND C(L) < > 84 AND C(L) < > 20 AND C(L)
< > 19 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
1840
1830 GOTO 1850
1840 IF C(L) < > 25 AND C(L) < > 89 AND C(L) < > 10 AND C(L) < > 74 AND C(L)
< > 9 AND C(L) < > 73 AND C(L) < > 78 GOTO 1450
1850 IF C(L) = 33 OR C(L) = 83 OR C(L) = 19 GOTO 1870
1860 L = L + 2: GOTO 1820
1870 A(56) = A(56) + C(L + 1) - C(K + 1): A(60) = A(60) + C(L + 1) - C(K +
1): A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
1880 REM TIME ON SIB1
1890 L = K + 2
1900 IF C(L) < > 33 AND C(L) < > 68 AND C(L) < > 84 AND C(L) < > 20 AND C(L)
< > 4 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
1920
1910 GOTO 1930
1920 IF C(L) < > 25 AND C(L) < > 89 AND C(L) < > 11 AND C(L) < > 75 AND C(L)
< > 15 AND C(L) < > 79 AND C(L) < > 77 GOTO 1450
1930 IF C(L) = 33 OR C(L) = 68 OR C(L) = 4 GOTO 1950
1940 L = L + 2: GOTO 1900
1950 A(57) = A(57) + C(L + 1) - C(K + 1): A(61) = A(61) + C(L + 1) - C(K +
1): A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
1960 REM TIME ON SIB2
1970 L = K + 2
1980 IF C(L) < > 33 AND C(L) < > 70 AND C(L) < > 84 AND C(L) < > 20 AND C(L)
< > 6 AND C(L) < > 37 AND C(L) < > 45 AND C(L) < > 55 AND C(L) < > 56 GOTO
2000
1990 GOTO 2010
2000 IF C(L) < > 25 AND C(L) < > 89 AND C(L) < > 12 AND C(L) < > 76 AND C(L)
< > 16 AND C(L) < > 80 AND C(L) < > 44 GOTO 1450
2010 IF C(L) = 33 OR C(L) = 70 OR C(L) = 6 GOTO 2030
2020 L = L + 2: GOTO 1980

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2030 A(58) = A(58) + C(L + 1) - C(K + 1):A(62) = A(62) + C(L + 1) - C(K +
1):A(63) = A(63) + C(L + 1) - C(K + 1): GOTO 630
2040 A(68) = A(68) + 1:A(67) = A(67) + 1: IF MID$(PO$,SN,1) = "M" THEN MC =
70 + NC:A(MC) = A(MC) + 1:A(76) = A(76) + 1
2050 GOTO 630
2060 A(69) = A(69) + 1:A(67) = A(67) + 1: IF MID$(PO$,SN,1) = "M" THEN MC =
73 + NC:A(MC) = A(MC) + 1:A(76) = A(76) + 1
2070 GOTO 630
2080 NEXT SN
2090 IF C$ = "N" GOTO 2170
2100 PRINT D$;"OPEN ";E$
2110 PRINT D$;"APPEND ";E$
2120 PRINT D$;"WRITE ";E$
2130 FOR I = 0 TO 76
2140 PRINT A(I)
2150 NEXT I
2160 PRINT D$;"CLOSE ";E$
2170 PRINT : PRINT "--NO OF REJECTIONS TO INFANT 1--"
2180 PRINT : PRINT "BY MOTHER ";A(0)
2190 PRINT : PRINT "BY FATHER ";A(1)
2200 PRINT : PRINT "BY SIB 1 ";A(2)
2210 PRINT : PRINT "BY SIB 2 ";A(3)
2220 PRINT : PRINT "--NO OF REJECTIONS TO INFANT 2--"
2230 PRINT : PRINT "BY MOTHER ";A(4)
2240 PRINT : PRINT "BY FATHER ";A(5)
2250 PRINT : PRINT "BY SIB 1 ";A(6)
2260 PRINT : PRINT "BY SIB 2 ";A(7)
2270 PRINT : PRINT "TOTAL NO OF REJECTIONS ";A(8)
2280 PRINT : PRINT "--NO OF DISTRESS CALLS--"
2290 PRINT : PRINT "BY INFANT 1 ";A(9)
2300 PRINT : PRINT "BY INFANT 2 ";A(10)
2310 PRINT : PRINT "TOTAL NO OF DISTRESS CALLS ";A(11)
2320 PRINT : PRINT "--DURATION OF DISTRESS CALLS--"
2330 PRINT : PRINT "BY INFANT 1 ";A(12)
2340 PRINT : PRINT "BY INFANT 2 ";A(13)
2350 PRINT : PRINT "TOTAL DURATION OF DISTRESS CALLS ";A(14)
2360 PRINT : PRINT "--NO OF CLIMB-ONS BY INFANT 1--"
2370 PRINT : PRINT "ON MOTHER ";A(15)
2380 PRINT : PRINT "ON FATHER ";A(16)
2390 PRINT : PRINT "ON SIB 1 ";A(17)
2400 PRINT : PRINT "ON SIB 2 ";A(18)
2410 PRINT : PRINT "--NO OF CLIMB-ONS BY INFANT 2--"

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2420 PRINT : PRINT "ON MOTHER ";A(19)
 2430 PRINT : PRINT "ON FATHER ";A(20)
 2440 PRINT : PRINT "ON SIB 1 ";A(21)
 2450 PRINT : PRINT "ON SIB 2 ";A(22)
 2460 PRINT : PRINT "TOTAL NO OF CLIMB-ONS ";A(23)
 2470 PRINT : PRINT "--NO OF PICK-UPS OF INFANT 1--"
 2480 PRINT : PRINT "BY MOTHER ";A(24)
 2490 PRINT : PRINT "BY FATHER ";A(25)
 2500 PRINT : PRINT "BY SIB 1 ";A(26)
 2510 PRINT : PRINT "BY SIB 2 ";A(27)
 2520 PRINT : PRINT "--NO OF PICK-UPS OF INFANT 2--"
 2530 PRINT : PRINT "BY MOTHER ";A(28)
 2540 PRINT : PRINT "BY FATHER ";A(29)
 2550 PRINT : PRINT "BY SIB 1 ";A(30)
 2560 PRINT : PRINT "BY SIB 2 ";A(31)
 2570 PRINT : PRINT "TOTAL NO OF PICK-UPS ";A(32)
 2580 PRINT : PRINT "--NO OF CLIMB-OFFS BY INFANT 1--"
 2590 PRINT : PRINT "FROM MOTHER ";A(33)
 2600 PRINT : PRINT "FROM FATHER ";A(34)
 2610 PRINT : PRINT "FROM SIB 1 ";A(35)
 2620 PRINT : PRINT "FROM SIB 2 ";A(36)
 2630 PRINT : PRINT "--NO OF CLIMB-OFFS BY INFANT 2--"
 2640 PRINT : PRINT "FROM MOTHER ";A(37)
 2650 PRINT : PRINT "FROM FATHER ";A(38)
 2660 PRINT : PRINT "FROM SIB 1 ";A(39)
 2670 PRINT : PRINT "FROM SIB 2 ";A(40)
 2680 PRINT : PRINT "TOTAL NO OF CLIMB-OFFS ";A(41)
 2690 PRINT : PRINT "--NO OF TIMES INFANT 1 RUBBED OFF--"
 2700 PRINT : PRINT "BY MOTHER ";A(42)
 2710 PRINT : PRINT "BY FATHER ";A(43)
 2720 PRINT : PRINT "BY SIB 1 ";A(44)
 2730 PRINT : PRINT "BY SIB 2 ";A(45)
 2740 PRINT : PRINT "--NO OF TIMES INFANT 2 RUBBED OFF--"
 2750 PRINT : PRINT "BY MOTHER ";A(46)
 2760 PRINT : PRINT "BY FATHER ";A(47)
 2770 PRINT : PRINT "BY SIB 1 ";A(48)
 2780 PRINT : PRINT "BY SIB 2 ";A(49)
 2790 PRINT : PRINT "TOTAL NO OF RUB-OFFS ";A(50)
 2800 PRINT : PRINT "--INFANT 1 DURATION OF TIME ON--"
 2810 PRINT : PRINT "MOTHER ";A(51)
 2820 PRINT : PRINT "FATHER ";A(52)
 2830 PRINT : PRINT "SIB 1 ";A(53)
 2840 PRINT : PRINT "SIB 2 ";A(54)


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2850 PRINT : PRINT "--INFANT 2 DURATION OF TIME ON--"
2860 PRINT : PRINT "MOTHER ";A(55)
2870 PRINT : PRINT "FATHER ";A(56)
2880 PRINT : PRINT "SIB 1 ";A(57)
2890 PRINT : PRINT "SIB 2 ";A(58)
2900 PRINT : PRINT "--TOTAL DURATION OF TIME ON--"
2910 PRINT : PRINT "MOTHER ";A(59)
2920 PRINT : PRINT "FATHER ";A(60)
2930 PRINT : PRINT "SIB 1 ";A(61)
2940 PRINT : PRINT "SIB 2 ";A(62)
2950 PRINT : PRINT "TOTAL DURATION OF TIME ON ";A(63)
2960 PRINT : PRINT "TOTAL NO OF GRID LINE CROSSES ";A(67)
2970 PRINT : PRINT "NO OF HORIZONTAL CROSSES ";A(68)
2980 PRINT : PRINT "NO OF VERTICAL CROSSES ";A(69)
2990 PRINT : PRINT "--NO OF HORIZONTAL CROSSES BY MOTHER--"
3000 PRINT : PRINT "WITH 0 INFANTS ";A(70)
3010 PRINT : PRINT "WITH 1 INFANT ";A(71)
3020 PRINT : PRINT "WITH 2 INFANTS ";A(72)
3030 PRINT : PRINT "--NO OF VERTICAL CROSSES--"
3040 PRINT : PRINT "WITH 0 INFANTS ";A(73)
3050 PRINT : PRINT "WITH 1 INFANT ";A(74)
3060 PRINT : PRINT "WITH 2 INFANTS ";A(75)
3070 PRINT : PRINT "TOTAL NO OF GRID CROSSES BY MOTHER ";A(76)
3080 PRINT
3090 PRINT D$;"PR=0"
3100 END
3110 X$ = MID$(PO$,SN,1)
3120 IF X$ = "M" AND C(K) < > 17 AND C(K) < > 81 AND C(K) < > 1 AND C(K) < >
65 AND C(K) < > 90 AND C(K) < > 21 AND C(K) < > 85 AND C(K) < > 8 AND C(K) <
> 45 GOTO 3140
3130 GOTO 3270
3140 IF X$ = "M" AND C(K) < > 20 AND C(K) < > 84 AND C(K) < > 25 AND C(K) <
> 89 AND C(K) < > 55 AND C(K) < > 56 AND C(K) < > 72 AND C(K) < > 66 GOTO
3290
3150 GOTO 3270
3160 IF X$ = "F" AND C(K) < > 23 AND C(K) < > 87 AND C(K) < > 19 AND C(K) <
> 83 AND C(K) < > 88 AND C(K) < > 9 AND C(K) < > 73 AND C(K) < > 10 AND C(K)
< > 45 GOTO 3180
3170 GOTO 3270
3180 IF X$ = "F" AND C(K) < > 20 AND C(K) < > 84 AND C(K) < > 25 AND C(K) <
> 89 AND C(K) < > 55 AND C(K) < > 56 AND C(K) < > 74 AND C(K) < > 78 GOTO
3290

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3190 GOTO 3270
3200 IF X$ = "X" AND C(K) < > 5 AND C(K) < > 69 AND C(K) < > 4 AND C(K) < >
68 AND C(K) < > 67 AND C(K) < > 15 AND C(K) < > 79 AND C(K) < > 11 AND C(K)
< > 45 GOTO 3220
3210 GOTO 3270
3220 IF X$ = "X" AND C(K) < > 20 AND C(K) < > 84 AND C(K) < > 25 AND C(K) <
> 89 AND C(K) < > 55 AND C(K) < > 56 AND C(K) < > 75 AND C(K) < > 77 GOTO
3290
3230 GOTO 3270
3240 IF X$ = "Y" AND C(K) < > 18 AND C(K) < > 82 AND C(K) < > 6 AND C(K) < >
70 AND C(K) < > 86 AND C(K) < > 16 AND C(K) < > 80 AND C(K) < > 12 AND C(K)
< > 45 GOTO 3260
3250 GOTO 3270
3260 IF X$ = "X" AND C(K) < > 20 AND C(K) < > 84 AND C(K) < > 25 AND C(K) <
> 89 AND C(K) < > 55 AND C(K) < > 56 AND C(K) < > 76 AND C(K) < > 44 GOTO
3290
3270 FL = 0
3280 RETURN
3290 PRINT : PRINT "SESSION ";SN;"RECORD ";K;" KEY PRESS FOR WRONG
FOCAL ANIMAL "
3300 FL = 1
3310 RETURN

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